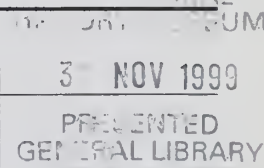


# A new stylophoran echinoderm, *Juliaecarpus milnerorum*, from the late Ordovician Upper Ktaoua Formation of Morocco

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**SYNOPSIS.** The late Ashgill stylophoran echinoderm *Juliaecarpus milnerorum* gen. et sp. nov. from the Upper Ktaoua Formation of Morocco is characterized by a high degree of thecal symmetry, a large suranal plate and an almost bilaterally symmetrical arrangement of supracentralia on the anterior half of the theca. *Juliaecarpus* was adapted to resting on a soft sea bottom by exploiting the weight-bearing capacity of mud. Locomotion probably occurred through alternating left and right lateral thrusts of the styloid and ossicular spikes against sediment, separated by upward and downward return strokes. In most classifications, *Juliaecarpus* would be placed in the cornutes, owing to the presence of a zygial bar extending from  $M'_1$  to the right posterior part of the thecal frame and to the fact that the marginalia are rod-like and surround several supracentralia and infracentralia. Following recent classifications, however, *Juliaecarpus* is best regarded as an ankyroid, due to its almost bilaterally symmetrical outline, to the possession of styloid processes and to the fact that the posterior zygial plate is a somatic element sutured with the posterior right part of the thecal frame, but not included in the latter. Among ankyroids, *Reticulocarpus hanusi*, *Beryllia miranda* and *Domfrontia pissotensis* most closely resemble *Juliaecarpus*.

## INTRODUCTION

### The stylophoran controversy

The debated systematic affinities of the stylophorans, a problematic group of marine metazoans of the Palaeozoic covered with an echinoderm-like skeleton of stereomic calcite (Smith, 1980) and variously allied to the echinoderms (e.g. Ubaghs, 1968) or to the chordates (e.g. Jefferies, 1986), have generated great interest in recent years, resulting in the publication of several papers in which their alpha taxonomy as well as their relationships (both within the group and in the context of deuterostome phylogeny) are discussed. Gee (1996) provided updated bibliographical references and a com-

prehensive review of the controversy surrounding these animals. The most recent account of the debate is the scientific correspondence between Peterson (1995) and Jefferies (1997) (but see also Sumrall, 1997 for comments).

Different opinions as to which thecal surfaces and marginal thecal plates are homologous in the two stylophoran groups of the cornutes (Jaekel, 1901) and the mitrates (Jaekel, 1918), as well as disagreement on their anatomical orientation and on the function of their single and jointed exothecal appendage, have led to a proliferation of different and often contrasting morphological terminologies. An additional difficulty is the lack of a standardized plate nomenclature (Caster, 1952; Ubaghs, 1968, 1969, 1981; Jefferies, 1968, 1973, 1981, 1986, 1997; Jefferies & Prokop, 1972; Jefferies & Lewis,

1978; Philip, 1979; Kolata & Jollie, 1982; Kolata *et al.*, 1991; Parsley, 1988, 1991, 1994, 1997, 1998; Ruta, 1998, in press).

Parsley (1997, 1998) and Lefebvre *et al.* (1998) addressed the problematic nature of the stylophorans in a number of papers focussing on their skeletal homologies and interrelationships. In particular, the elegant synthesis by Lefebvre *et al.* (1998) adds to the arguments put forward by earlier authors (e.g. Ubaghs, 1968, 1969, 1981; Parsley, 1988, 1991; Kolata *et al.*, 1991) in support of the homology between the plano-concave thecal surface of the mitrates and the flat thecal surface of the cornutes. Such arguments are based on a detailed comparative morphological study of the following skeletal structures in representatives of both stylophoran groups: 1) the tripartite, jointed exothecal appendage; 2) the apophyses, which project medially from the most anterior pair of marginal thecal plates,  $M'_1$  and  $M_1$ ; 3) the left and right adoral plates, LA and RA, which contribute to the excavation for the insertion of the articulated appendage together with the apophyses; and 4) the zygale/septum complex, which runs obliquely on the flat side of the theca and, at least in its anterior portion, is associated with the same marginal plate ( $M'_1$ ) in all known stylophorans (see also section on the terminology below).

The constructional and topological similarity of the above-mentioned structures in cornutes and mitrates leads to the unequivocal conclusion that all stylophorans show the same basic anatomical organization (Ubaghs, 1981; Kolata *et al.*, 1991; Peterson, 1995; Parsley, 1997, 1998; Lefebvre *et al.*, 1998), contrary to the opinion expressed by such workers as Jefferies (1986 and references therein), Cripps (1989a) and Cripps & Daley (1994).

The recent discovery of such primitive mitrates as *Vizcainocarpus dentiger* Ruta, 1997 and a morphological comparison between this species and the cornute *Nanocarpus dolambii* Ubaghs, 1991 strengthen the commonly held view that the flat side of the cornute theca corresponds to the plano-concave side of the mitrate theca. However, this view was formerly rejected by me (Ruta, 1997; see also discussion in Ruta, 1998, in press) and I did not compare *Vizcainocarpus* with *Nanocarpus*. In addition, I presented a character-based hypothesis of interrelationships of the mitrocystitid mitrates using several cornute taxa as outgroups, but I neglected most skeletal similarities between cladistically derived cornutes and basal mitrates.

Additional arguments favouring the homology of the flat thecal surfaces in all stylophorans were presented by Ubaghs (1994) in his comparison between the cornute *Lyricocarpus courtessolei* and the mitrate *Chinianocarpus thoralii* Ubaghs, 1961.

After the publication of my 1997 paper on *Vizcainocarpus*, Dr B. Lefebvre (pers. comm.) and Prof R. L. Parsley (pers. comm.) drew my attention to the fundamental resemblance (especially evident in the zygale/septum complex) between the flat thecal surface of *Vizcainocarpus* and that of *Nanocarpus* as well as to the fact that the distinction between cornutes and mitrates, as proposed by those workers who interpret stylophorans as chordates, relies on *ad hoc* hypotheses of character transformation between these two groups (see also below), as previous authors have already pointed out (notably Ubaghs, 1981, Kolata *et al.*, 1991 and Parsley, 1991).

In fact, as noted by Parsley (1997, 1998) and especially Lefebvre *et al.* (1998), the distinction between cornutes and mitrates is no longer valid and ought to be abandoned in favour of the resolution of phylogenetic relationships of all stylophorans as a group. Revisionary work in this field has just begun (Dr. B. Lefebvre, pers. comm.; Ms M. Martí-Mus, pers. comm.). In particular, Parsley (1997, 1998) showed that the mitrates, as originally conceived, may not have a common origin after all (i.e. mitrates would be polyphyletic). These results prompt a re-evaluation of current ideas on the evolution and

character distribution of these fossils (however, see below for comments on the results of Parsley's (1997, 1998) analysis).

## The stylophoran interpretation adopted

In the present paper, the stylophorans are interpreted as echinoderms, according to the traditional view and contrary to the opinions expressed in some of my earlier works, in which a chordate interpretation was followed and in which the jointed appendage of these animals was regarded as a posterior, locomotory organ, homologous with a chordate tail (references in Ruta, 1998, in press). I now concur with several other researchers that the segmented appendage of cornutes and mitrates, henceforth referred to as the aulacophore (Ubaghs, 1968), is primarily an anterior feeding organ of ambulacral origin, although, as Sumrall (1997: 269) pointed out, the resemblance between the aulacophore and the ambulacrum '... does not allow for the falsification of the hypothesis that [these two structures] are homologous'.

The interpretation of the aulacophore as an echinoderm arm fully satisfies criteria of morphological similarity. Thus, for Lefebvre *et al.* (1998: 104) the aulacophore '... may be homologous to a single crinoid arm'. However, this view has been emphatically rejected by some authors, notably Jefferies (1986) and Gee (1996). The arguments in support of the echinoderm affinities of the stylophorans are thoroughly discussed by Ubaghs (1968, 1981), Parsley (1988, 1991, 1994, 1997, 1998) and Lefebvre *et al.* (1998) and will not be repeated in this paper.

Unlike Ubaghs (1981) and in partial agreement with other authors, I also regard the aulacophore as a locomotory device which may have functioned in different ways in different stylophorans (e.g. Jefferies & Prokop, 1972; Kolata & Jollie, 1982; Jefferies, 1984, 1986; Parsley, 1988, 1991; Cripps, 1989a; Kolata *et al.*, 1991; Daley, 1992; Woods & Jefferies, 1992; Ruta & Bartels, 1998).

A third interpretation of the aulacophore, considered only as a locomotory device but not homologous with a chordate tail, was discussed by Philip (1979), Kolata & Jollie (1982) and Kolata *et al.* (1991) (synthesis in Jefferies, 1986 and Ruta, 1998, in press).

The calcichordate theory of Jefferies and co-workers (see especially Jefferies, 1986) deserves a final, brief comment. It represents a thorough elaboration of Gislén's (1930) hypothesis that the ancestry of the vertebrates is rooted into the extinct assemblage of the 'carpodid echinoderms', encompassing today the groups solutes, cornutes, mitrates, cinctans and ctenocystoids, and was dealt with at length by Gee (1996). According to the calcichordate theory, most solutes (see Daley, 1996) and all cornutes are seen as stem-group chordates, all mitrates as stem-group members of the three modern chordate subphyla, Tunicata, Acraniata and Craniata, and cinctans and ctenocystoids as stem-group echinoderms.

As far as the stylophorans (cornutes and mitrates) are concerned, the calcichordate theory requires radical internal and external anatomical changes in passing from the cornutes to the mitrates, notably the loss of the mid and distal portion of the cornute aulacophore and a re-organization of the remaining, proximal portion into the very similar tripartite structure observed in the mitrates. Ubaghs (1981), Parsley (1991) and Lefebvre *et al.* (1998) emphasized the difficulties associated with the anatomical modifications demanded by Jefferies' theory. Such modifications are supported by dubious or, more often, no fossil evidence at all. Thus, as Lefebvre *et al.* (1998: 104) put it, acceptance of Jefferies' (1986) arguments implies that '... the median and distal parts of the aulacophore suddenly disappeared in the cornutes to reappear exactly identical but upside-down in mitrates'.

Despite my own initial convictions (references in Ruta, 1998, in



press), I now remain very sceptical when it comes to a consideration of the fossil evidence favouring the calcichordate interpretation of the stylophorans. Such an interpretation discounts obvious morphological and topological similarities between the anatomical organization of cornutes and that of mitrates and makes poorly supported or unsubstantiated claims as to the morphological changes which occurred at the cornute-mitrate transition (summary in Jefferies, 1986 and Cripps, 1989a).

The wealth of morphological data produced by Jefferies and co-workers is impressive. However, the morphological comparative analysis of the relevant fossils poses certain problems, especially as far as the anatomical evidence in support of the transition from cornutes to mitrates is concerned. The theory is, therefore, rejected in favour of widely accepted and well-corroborated views on skeletal homologies in the stylophorans.

## Terminology

Morphological nomenclature, plate notation and anatomical orientation of the stylophorans are those proposed by Ubaghs (1968) in the *Treatise on Invertebrate Paleontology* (see also Ubaghs, 1969) and adopted by subsequent workers (e.g. Parsley, 1988, 1991, 1994, 1997, 1998, Sumrall *et al.*, 1997, Lefebvre *et al.*, 1998, etc.). The identification of the marginal plates in the new stylophoran described here is based on a recent character analysis by Parsley (1997, 1998) and on a comparative study of morphological data gleaned from various sources, especially Ubaghs (1968, 1969), Jefferies & Prokop (1972), Cripps (1989a), Cripps & Daley (1994) and Lefebvre *et al.* (1998).

A list of the morphological terms applied to the stylophorans and a detailed description of their external and internal anatomical organization were provided by Ubaghs (1968). I emphasize the fact that, in most cases, such a terminology does not imply anatomical or functional interpretations of the observed structures. As stated by Ubaghs (1968), the interpretations are often entirely conjectural (see, however, Jefferies, 1986 and discussion in Ruta, 1998, in press).

The most frequently cited morphological terms used in the anatomical description (Fig. 1) are briefly explained below and appear in bold in this section of the paper only. Most of them apply to all stylophorans, a few are restricted to the vast majority of these fossils and some are introduced here in conjunction with the description of the new taxon.

A stylophoran is divided morphologically into a posterior **theca** and an anterior **aulacophore**, the latter representing an arm (i.e. a feeding organ of ambulacral origin extending beyond the oral surface; see Sumrall, 1997). The convex and flat surfaces of the theca consist of a **dorsal integument** and a **ventral integument** respectively. The main thecal opening, at the opposite end of the theca with respect to the aulacophore insertion, is the **anus**. The **main axis**, or **longitudinal axis** of the body, is the intersection between the plane of bilateral symmetry of the aulacophore and the plane of flattening of the theca. The **oro-anal axis** runs from the centre of the aulacophore insertion to the anus. **Proximal** and **distal** indicate the position of a structure close to or away from the junction between the theca and the aulacophore. **Median**, **admedian** and **lateral** (or **marginal**) indicate the position of thecal structures (e.g. integument plates) with respect to the longitudinal axis.

The theca is framed by **marginal plates**, or **marginalia**, surrounding several **central plates**, or **centralia**, termed **supracentralia** and **infracentralia** on the dorsal and ventral surfaces respectively. The **marginalia** are labelled antero-posteriorly (i.e. from the thecal excavation for the aulacophore insertion to the anus) as  $M'_1, M'_2, M'_3, \dots$ , etc. on the left side, and as  $M_1, M_2, M_3, \dots$ , etc. on the right side

of the theca. Each marginal plate consists of a **dorso-lateral projection**, sloping laterally and ventrally, and a **ventral projection**. The two projections meet at the lateral margins of the theca. The two anterior supracentral plates articulated with  $M'_1$  and  $M_1$  and contributing to the excavation for the aulacophore insertion are the left and right **adoral plates**, or **adoralia** (LA and RA respectively).

A large, flexibly articulated plate (perhaps an enlarged supracentral element) present between the rearmost ends of the thecal margins and roofing over the anal opening in the new stylophoran described here is termed the **suranal plate**, or **suranal**.

The **zygal bar**, or **zygal** (apparently absent in such cornute genera as *Ceratocystis* Jaekel, 1901 and, perhaps, also *Nevadaecystis* Ubaghs, 1968 and *Protocystites* Hicks, 1872; see also Ubaghs, 1963, 1967, 1987, Jefferies, 1969, 1986 and Jefferies *et al.*, 1987), is a strut-like bar connecting  $M'_1$  with the posterior part of the right margin of the theca on the ventral surface and is homologous with the septum of mitrates (Ubaghs, 1968, 1969; Kolata & Jollie, 1982; Kolata *et al.*, 1991; Parsley, 1991, 1997, 1998; Lefebvre *et al.*, 1998). In several stylophorans, such as the new form described in this work, the zygal consists of a **posterior zygal plate** (a somatic element sutured with the right posterior part of the thecal frame but not included in the latter) and a **posterior process** of  $M'_1$ .

The proximal part of the aulacophore usually consists of **tetramerous rings**, each composed of a pair of dorsal plates, termed the **tectals**, and a pair of ventral plates, or **inferolaterals**. The robust ventral element present in the intermediate part of the aulacophore is the **styloid** or **stylocone**. The term styloid is preferred over stylocone when the structure in question bears well-developed projections (spikes, cusps, blades, etc.), as in mitrates and in several mitrate-like cornutes (Jaekel, 1918; Parsley, 1991, 1997, 1998; Lefebvre *et al.*, 1998). However, the distinction between stylocone and styloid has no morphological basis, as correctly pointed out by Ubaghs (1968, 1981), for these terms refer to the same (homologous) skeletal element in all stylophorans. Such a distinction was adopted by Jefferies (1986) who denied the homology between the cornute stylocone and the mitrate styloid (but see rebuttal by Lefebvre *et al.*, 1998), as explained above.

Each segment of the distal part of the aulacophore consists of a ventral **ossicle** articulated with a dorsal pair of **cover plates**. The structures visible on the internal surface of the aulacophore ossicles and those present on the dorsal (internal with respect to the inside of the theca) surface of the most anterior portions of  $M'_1$  and  $M_1$  will be discussed separately in the descriptive anatomical section of this paper.

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## AIMS OF THE STUDY

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### Background

In the collections of the Department of Palaeontology, The Natural History Museum, London, there is abundant material of a new stylophoran echinoderm from upper Ashgill mudstones in Morocco, collected in the early 1990s. Several features of its dorsal and ventral integuments, thecal frame and aulacophore justify its attribution to a new genus and species, although it is similar in several respects to such mitrate-like cornutes as *Reticulocarpos hanusi* Jefferies & Prokop, 1972, *Domfrontia pissotensis* (Chauvel & Nion, 1977) and *Beryllia miranda* Cripps & Daley, 1994 (see section on morphological comparisons below).

In traditional classifications of the stylophorans (e.g. Ubaghs, 1968), the fossils described herein would be assigned to the cornutes, because it possesses a zygal bar extending from plate  $M'_1$  to the right

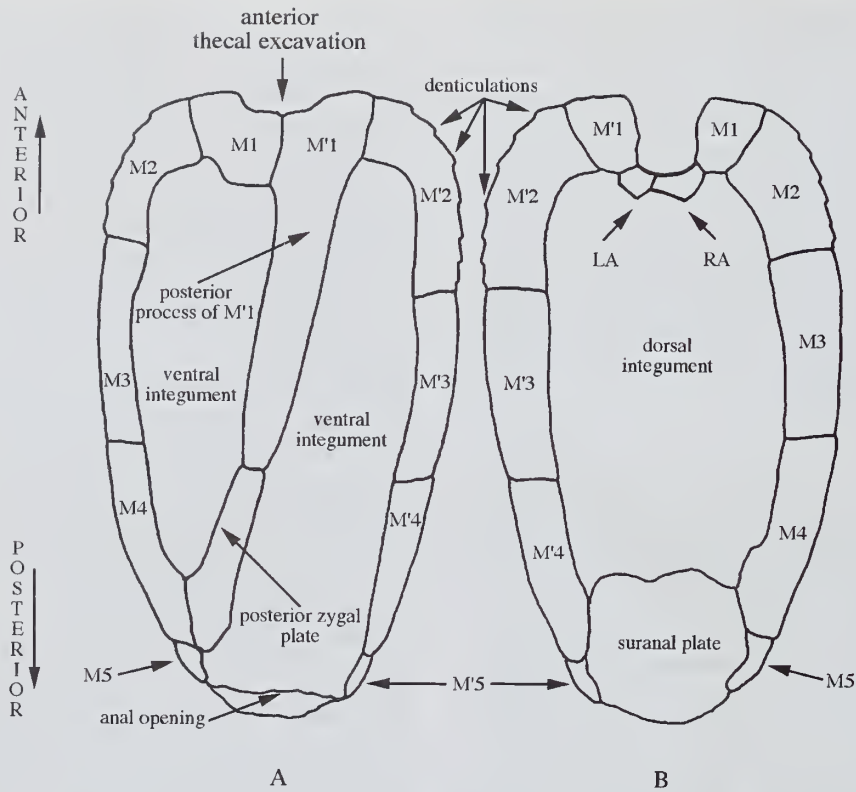


Fig. 1 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Schematic reconstruction showing orientation, anatomical nomenclature and plate terminology of the theca. A, ventral aspect. B, dorsal aspect.

posterior part of the thecal frame, because its marginal plates are elongate and rod-like and because its dorsal and ventral integuments consist of a relatively large number of plates. In Parsley's (1997, 1998) recent phylogenetic analysis, the above-mentioned taxa to which the new Moroccan form bears close resemblance, several other almost bilaterally symmetrical and mitrate-like cornutes and all the mitrates are set apart from the strongly asymmetrical (and often boot-shaped) cornutes and are given a rank of their own, for which Parsley (1997, 1998) proposed the name Ankyroidea. The new Moroccan taxon would be an ankyroid according to Parsley's (1997, 1998) phylogenetic scheme.

The order Ankyroidea comprises stylophorans in which the thecal outline approaches bilateral symmetry in varying degrees, the posterior zygial plate is usually a separate somatic element (i.e. this plate is not part of the marginal frame of the theca) and the styloid bears projections in the form of spikes, cusps or blades. However, stylophorans other than the ankyroids form a paraphyletic assemblage in Parsley's (1997, 1998) phylogeny. Parsley (1997, 1998) retained the former name Cornuta as emended by Ubahgs (1968) for this assemblage (not characterizable in the light of shared derived features), but suppressed the Mitrata.

The present study aims to: 1) reconstruct and describe a late Ordovician Moroccan ankyroid; 2) discuss its morphology from a functional viewpoint, with emphasis placed on the stability of the animal in water currents and on the feeding and locomotory roles of its aulacophore; 3) compare it with several other Ordovician ankyroids.

The discovery of the new Moroccan taxon prompts a reassessment

of stylophoran interrelationships as well as a critical analysis of the cornute-mitrate transition (Cripps, 1989a, b, 1991; Daley, 1992; Cripps & Daley, 1994) in the light of more traditional views on homologous skeletal characters in these echinoderms. Such arguments will be developed in another paper.

## Material and methods

Most specimens are preserved as incomplete, slightly to heavily disrupted external moulds of the theca and aulacophore. Incomplete internal moulds of isolated thecal elements (especially marginalia) and, more rarely, of almost complete thecae have also been recorded. In very few individuals, the thecae are fully articulated and the degree of disruption affects mainly the alignment of the left and right marginalia. The dorsal integument is usually completely preserved, both externally and, more rarely, internally. The ventral integument, on the other hand, is invariably poorly preserved, heavily disrupted or missing and the boundaries between the infracentralia are difficult to observe. The posterior end of the theca is generally disrupted.

The zygial bar is often found broken, but in some individuals, both the posterior zygial plate and the posterior process of  $M'_1$  are uncrushed and their relative size and proportions with respect to the rest of the theca can be accurately reconstructed. The loss of supracentralia in few specimens allows the dorsal surface of the zygial bar (and especially its suture with the thecal frame) to be observed. Sometimes, compaction of the fossils resulted in the squashing of the supracentralia against the zygial bar, thus reproducing the boundaries of the latter and the nature of the contact of the distal end of the



posterior zygial plate with the posterior part of the right thecal margin. Numerous isolated marginal elements reveal details of their stereom texture and the degree of curvature of their internal surfaces (i.e. the surfaces oriented towards the internal side of the theca).

Rarely is the aulacophore found in place. Its proximal part, when preserved, is invariably incomplete or crushed. Its intermediate and distal parts are sometimes found articulated with each other and slightly disrupted. More often, only disarticulated styloids, cover plates and ossicles are found.

The fine matrix in which the skeletal moulds occur reproduces changes in the stereom texture of various skeletal elements, both externally and internally. In some cases, the external surface of the specimens appears to be heavily weathered and covered with a network of criss-crossed cracks, often obliterating almost completely both plate boundaries and skeletal fabric.

The fossil material required little mechanical preparation. Some specimens were dissected with a needle to partially expose the appendage and the peripheral margins of the thecal frame. Almost all specimens were cast with black-stained latex. Latex peels were coated with ammonium chloride sublimate and photographed at a low angle of illumination to emphasize details of the external skeletal surface (see also Ruta & Bartels, 1998).

The reconstruction of the external aspect of the animal and of several details of its external and internal anatomy (e.g. suranal plate, apophyses, internal surface of  $M'_1$ , peripheral flange, styloid, ossicles, etc.) are based on camera lucida sketches drawn to scale and on a series of engineering projections in dorsal, ventral, lateral, anterior and posterior views (Fig. 2A–E). The engineering drawings were based on morphological information gleaned mainly from the following specimens (see also list of the material examined below): BMNH EE 3069a, b, 3070a, b, 3072a, b, 3101a, b, 3115a, b, 3119a, b, 3127a, b, 3144a, b, 3163, 3178a, b. The cross-section of the marginalia was reconstructed from the latex peels by cutting these with a razor blade at different levels perpendicular to the direction of maximum elongation of each marginal plate. Observations were carried out using a Nikon SMZ–10 binocular microscope.

## SYSTEMATIC PALAEOLOGY

Phylum ECHINODERMATA Fleming, 1828  
Class STYLOPHORA Gill & Caster, 1960  
Order ANKYROIDA Parsley, 1997  
Family unassigned

REMARKS. As conceived by Parsley (1997, 1998), the order Ankyroida includes the former order Mitrata Jaekel, 1918 and some representatives of the former order Cornuta Jaekel, 1901, the latter almost universally considered as a paraphyletic group by stylophoran workers (e.g. Jefferies, 1986; Cripps, 1991; Daley, 1992; Woods & Jefferies, 1992; Cripps & Daley, 1994; Parsley, 1997, 1998; Lefebvre *et al.*, 1998). Although I am confident about the monophyly of the Ankyroida, I shall not elaborate upon the interrelationships between representatives of this group. These ought to be reassessed after the inclusion of several recently described taxa in a new, expanded character matrix for all known stylophorans.

I have not included a family in the systematic palaeontology section above. In this, I follow some systematists' view that traditional systematic categories ought to be abandoned (e.g. see discussion in Craske & Jefferies, 1989) and that hierarchically clustered clades within a monophyletic group do not need naming. This approach avoids the introduction of additional names in the

systematic literature and eliminates ambiguities resulting from continuous redefinitions of previously established taxonomic names. A rankless phylogenetic scheme is especially desirable in the case of extinct groups (such as stylophorans) with a very discontinuous fossil record, because the discovery of additional taxa and/or characters is likely to affect taxon relationships and character distribution to a considerable extent.

Because very few subgroups within the stylophorans can be shown to be monophyletic (see discussion in Ruta, 1998, in press), a subdivision of the whole class into taxonomic ranks seems to be inadvisable at present (but see also Caster, 1952 and Ubaghs, 1968, 1969). Current taxonomic subdivisions, especially for the cornutes (Cripps, 1991; Daley, 1992; Cripps & Daley, 1994), ought to be reconsidered. The major problem with them is the fact that they have been generated by character coding built upon assumptions of character transformation at the comute-mitrate transition (Lefebvre *et al.*, 1998). Assumption-laden choice of some characters, based on theory and process, also characterized a recently published data set of mine (Ruta, 1997).

The results of other phylogenetic analyses of the stylophorans as a group or of different subsets of them differ significantly. Thus, there is need for an integration of the various data sets and for a critical evaluation of the characters used.

In their monograph on Middle Ordovician cornutes from Normandy, Cripps & Daley (1994: 107) erected the family Reticulocarpidae, for which they provided the following diagnosis: 'The Reticulocarpidae are cornutes with optic embayments, slit-like terminal mouths, no branchial skeleton and ventral spikes on the mid- and hind-tail ossicles'. As I shall explain in detail below, the stylophoran described in the present work is extremely similar to the genus *Reticulocarpus*.

However, in the light of Parsley's (1997, 1998) cladistic analysis and of the various problems associated with Cripps' (1991) and Cripps & Daley's (1994) character coding, I question the sister group relationship between *Reticulocarpus hanusi* Jefferies & Prokop, 1972 and *Beryllia miranda* Cripps & Daley, 1994, grouped together in the Reticulocarpidae by Cripps & Daley (1994).

I am more inclined to accept Parsley's (1997, 1998) conclusion that *Reticulocarpus* and *Prokopicystis mergli* Cripps, 1989a are each other's closest relatives and that, together, they form the sister group of the genus *Hanusia* Cripps, 1989b (see also section on morphological comparisons below).

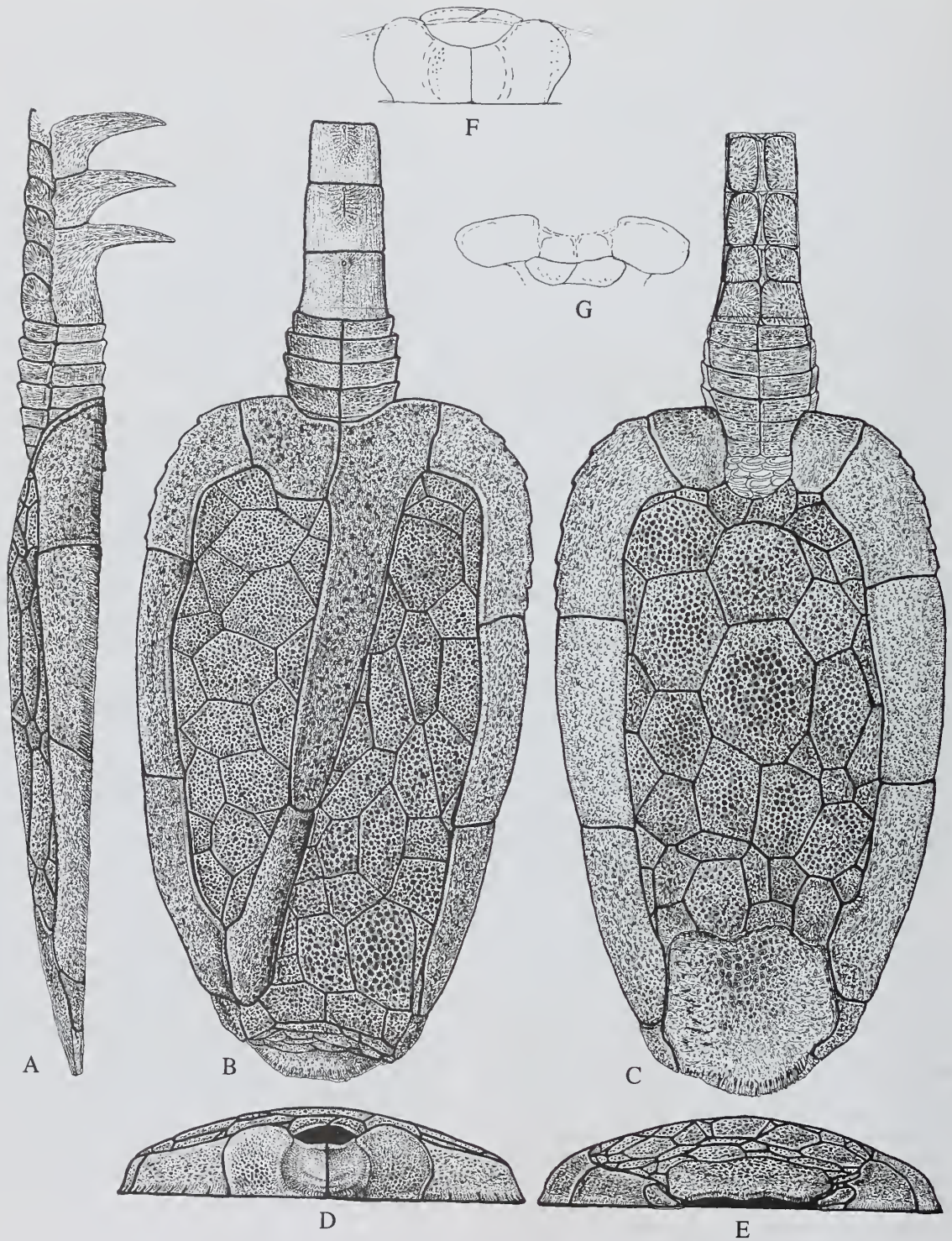
Parsley's (1997, 1998) data matrix likewise presents some problems (e.g. presence of some redundant characters, poorly defined states, low number of characters, wrong coding for certain features in some stylophoran taxa, etc.). Despite this, a preliminary parsimony analysis of Parsley's (1997, 1998) data matrix using PAUP version 3.1.1 (Swofford, 1993) (with inclusion of modified coding for several of his chosen characters, exclusion of redundant characters and corrections of several wrongly coded characters) produced results similar to those of his original run (the latter was based on reweighting of characters) and preserves in part the original tree structure. These results will be extensively discussed in a separate publication in conjunction with a revision of stylophoran interrelationships.

### Genus *JULIAECARPUS* nov.

TYPE SPECIES. *Juliaecarpus milnerorum* sp. nov.; late Ashgill (late Rawtheyan), Upper Ktaoua Formation, Morocco. The only known species.

DERIVATION OF NAME. After Julia J. Day (Department of Biology,





**Fig. 2** *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician. Upper Ashgill, Rawtheyan, Upper Ktaoua Formation. Morocco. Reconstruction of external aspect. **A**, right lateral view of theca and aulacophore. **B**, ventral view of theca and aulacophore. **C**, dorsal view of theca and aulacophore. **D**, anterior view of theca (aulacophore removed). **E**, posterior view of theca. **F**, schematic aspect of anterior thecal excavation showing apophyses and adoralia. **G**, schematic reconstruction of most anterior part of dorsal thecal surface showing adoralia and dorso-lateral projections of  $M'_1$  and  $M_1$ . Arrangement of integument plates, cover plates, tectals and inferolaterals is hypothetical.



University College, London), for her constant encouragement and for providing much useful advice. The suffix *-carpus* is a latinized version of the Greek word  $\chi\alpha\rho\pi\omicron\varsigma$  (carpos), fruit, gender masculine.

**DIAGNOSIS.** An ankyroid stylophoran echinoderm characterized by: extreme reduction in size of  $M'_5$  and  $M_3$ ; absence of dorsal bar between  $M'_4$  and  $M_4$ ; posterior zygial plate almost straight and with slightly expanded and flattened distal half; poorly pronounced denticulations present on lateral margins of  $M'_2$  and  $M_2$ ; nearly bilaterally symmetrical arrangement of subpolygonal supracentralia on anterior half of dorsal integument; occurrence of a large suranal plate of irregular and variable shape flexibly articulated with  $M'_4$ ,  $M_4$ ,  $M'_5$  and  $M_5$ .

*Juliaecarpus milnerorum* sp. nov. Figs 1–8, Pls 1–8

**DERIVATION OF NAME.** After Drs Andrew R. Milner (Department of Biology, Birkbeck College, University of London) and Angela C. Milner (Department of Palaeontology, The Natural History Museum, London), for their continuous support and exchange of ideas with the author over the years.

**HOLOTYPE.** The Natural History Museum, London: Department of Palaeontology, BMNH EE 3070a, b.

**PARATYPES.** The Natural History Museum, London: Department of Palaeontology, BMNH EE 3069a, b, 3071–2a, b, 3073–4, 3075a, b, 3079a, 3080–1a, b, 3083a, 3084–6, 3088–9, 3090, 3093–4, 3095a, b, 3098, 3101–4a, b, 3105, 3108–9a, b, 3111, 3113, 3114a, b, 3115a, b, 3116a, b, 3117, 3121–2, 3123a–c, 3124–5a, b, 3127a, b, 3129a, b, 3131–2a, b, 3134–7a, b, 3138–9, 3140–1a, b, 3143, 3144–7a, b, 3149a, 3150a, b, 3152a, b, 3153, 3155a, b, 3157, 3158a, b, 3160a, b, 3161, 3162a, b, 3163–4, 3166–7a, b, 3168a–c, 3169, 3170, 3171a, b, 3173a–c, 3175a, b, 3176–7, 3178a, b, 3180–1, 3183–4a, b.

**DIAGNOSIS.** As for the genus.

**LOCALITY.** Specimens were collected from locality 756 of Destombes (see also Chauvel, 1971), about 7 km west-south-west of Tazzarine, near Tiz n'Takhrît, Morocco. The reference map is Tazzarine Sheet of 1:100,000 topographical survey. The map coordinates are: x = 477,75; y = 417.

**HORIZON.** The fossil material occurs in light grey mudstones in the Upper Ktaoua Formation, which lies at the base of the southern part of the Ktaoua plain in the Moroccan Anti-Atlas. The formation consists mainly of grey-green arenaceous argillites interspersed with rare bands of oolitic iron or phosphatic nodules and varies in thickness from 70 m to 110 m.

Fossils are mainly concentrated in three different levels: a first level situated 30 m above the base of the formation and dominated by trinucleid and phacopid trilobites; a second level situated 10 m above the previous level and containing a trinucleid fauna; a third level encompassing the upper two-thirds of the formation, where a rare but well preserved and diverse fauna (more abundant than in the previous two levels) is recorded in widespread pelitic carbonate lenses.

The fauna of the Upper Ktaoua Formation includes, among the other taxa, several brachiopods (e.g. *Eostropheodonta intermedia*, *Eochonetes canaliferus*, *Chonetoidea radiatula*, *Comatopoma sororium*) and trilobites (e.g. *Baniaspis globosa*, *Brongniartella platynota marocana*, *Dreyfussina struvei*, *Eudolatites maiderensis*, *Flexicalymene ouzregui*, *Kloucecia poueytoi*, *Lichas marocanus*, *Mucronaspis greti*, *M. termieri*, *Actinopeltis* sp., *Amphitryon* sp., *Calymenella* sp., *Dionide* sp., *Onnia* sp., *Selenopeltis* sp., *Stenopareia* sp.), some echinoderms (e.g. *Destombesia diedra acuta*, *Echino-*

*sphaerites aurantium transversalis*, *Helicrinites ouguerfensis*, *Maghrebocystis pachythea cupuliformis*, *M. p. robusta*, 'Placocystites' *bohemicus*), rare conulariids, cephalopods, gastropods, bivalves, ostracods and abundant microplankton.

*Juliaecarpus milnerorum* (henceforth referred to as *Juliaecarpus* for brevity) comes from the third level.

**AGE.** Although most fossils in the Upper Ktaoua Formation are endemic, the fauna shows affinities with late Ashgill elements from the British Isles, Bohemia, Poland and Sweden. In particular, species belonging to certain genera of brachiopods (e.g. *Eostropheodonta*) and trilobites (e.g. *Brongniartella*, *Flexicalymene* and *Mucronaspis*) are extremely similar to congeneric species found in upper Ashgill rocks of northern, central and eastern Europe.

Destombes *et al.* (1985) suggested that the trinucleid trilobites (e.g. representatives of the genus *Onnia*) indicate an upper Rawtheyan age for the upper part of the Upper Ktaoua Formation, where *Juliaecarpus* occurs. Detailed palaeobiogeographical comparisons between late Ordovician faunas from different regions of the Mediterranean Province can be found in Destombes *et al.* (1985), Destombes & Willefert (1988) and Havlíček (1990).

With regards to *Juliaecarpus*, this stylophoran is very similar to several middle Ordovician and some late Ordovician ankyroids from France and Bohemia (e.g. the genera *Reticulocarpos*, *Beryllia* and *Domfrontia*; see also section on morphological comparisons below). Discoveries of other stylophorans from Morocco (e.g. Chauvel, 1971; Cripps, 1990; Beisswenger, 1994) strengthen the affinities between Ordovician North African faunistic elements and coeval fossil faunas from several European regions (see also Chauvel, 1981, 1986).

**OTHER REFERRED MATERIAL.** Chauvel (1971: 56, fig. 3f) briefly described a poorly preserved specimen of a stylophoran from the Upper Ktaoua Formation (Destombes Collection, no. 756c), provisionally referred by him to the family Kirkocystidae Caster, 1952 (formerly placed in the lagynocystid mitrates, but now generally referred to the peltocystid mitrates; Jefferies, 1973; Kolata *et al.*, 1991; Parsley, 1991). The specimen in question is the internal mould of a lower thecal surface displaying a considerable degree of disruption. Unfortunately, Chauvel's (1971) description was not accompanied by photographs and it is, therefore, difficult to ascertain the affinities of this fossil. Chauvel (1971) regarded it as an undetermined genus and labelled it as AVII.

Based on his line drawings, however, AVII may belong to *Juliaecarpus*. This is suggested by the relative proportions of the preserved marginalia, including the plate referred to by Chauvel (1971) as the posterior process, based on his attribution of the specimen to the kirkocystids. The plate in question may alternatively be interpreted as a posteriorly displaced posterior zygial plate. The relative size and proportions of the posterior process of  $M'_1$  with respect to the preserved marginalia are very similar to those observed in *Juliaecarpus*.

## ANATOMICAL DESCRIPTION

### Theca

**GENERAL ASPECT** (Figs 1, 2). The theca of *Juliaecarpus* consists of 10 marginal plates (or marginalia) forming a peripheral frame interrupted posteriorly at the level of the anal opening and showing an anterior excavation for the insertion of the aulacophore. The theca approaches a high degree of bilateral symmetry and is longer than wide, subelliptical to vaguely pyriform in outline and with a length/

width ratio of about 1.72. The maximum thecal width is at about two-fifths of the way posteriorly along the oro-anal axis.

A comparison between the maximum thecal sizes reported by Cripps & Daley (1994) in several solutes, cornutes and mitrates and the thecal sizes of some of the most complete and least disrupted specimens of *Juliaecarpus* shows that the latter ranks among the smallest stylophorans recorded to date. Estimated thecal length values in the best preserved specimens range between 7 mm and 10 mm, whereas thecal width values in the same specimens are comprised between 4 mm and 6 mm (see also Table 1). As discussed below, morphological variation, both in the general thecal proportions and in the shape and size of the individual plates, is small.

The lateral thecal margins are only slightly convex for most of their length, subparallel or gently diverging in their anterior half, slightly converging posteriorly and merging smoothly into the anterolateral, lobe-like angles of the theca. These are blunt and shaped approximately like an arc of about 90° in plan view. The left margin of the theca is slightly longer than the right margin, which suggests that the anal opening may have faced slightly rightward in life (see also Cripps & Daley, 1994). As a result of this difference in length, the oro-anal axis is not aligned with the longitudinal axis of the aulacophore, but is displaced slightly to the right of the latter.

A dorsal and a ventral integument, each composed of several polygonal plates of different shapes and sizes, are attached to the medial margins of the dorso-lateral and ventral projections of the marginalia. A large, irregularly polygonal supracentral element, the suranal plate, roofs over the anal opening and is interposed between the rearmost parts of the lateral thecal margins.

The boundaries of the anal opening could not be observed directly in any of the specimens examined, due to the extreme dorso-ventral flattening of the theca in its posterior third, to the generally poor preservation of the rearmost infracentralia and to the fact that the suranal plate is often found collapsed onto the internal side of the ventral thecal surface.

In some individuals, however, both the dorsal and the ventral thecal surfaces are preserved more or less fully articulated and a morphological comparison between part and counterpart suggests that the suranal plate either extended slightly beyond the posterior margin of the ventral integument or corresponded in position with the latter (see also description below). Thus, the anal opening faced either slightly ventralward or posteriorly in life and, as in most other ankyroids, was almost certainly slit-like, although the reconstruction of its outline is only tentative.

In longitudinal section, the theca of *Juliaecarpus* is shaped approximately like a hydrofoil (see also discussion on the morpho-functional adaptations of the theca in relation to the stability of the animal in water currents). The dorsal integument is likely to have been smoothly convex in lateral view and to have reached its maximum curvature at a point situated presumably slightly anterior to its central part. It probably sloped gently rearward and ventralward in life, as suggested by the fact that the height of the marginalia decreases uniformly antero-posteriorly, being about twice greater at the level of the anterior thecal excavation than at the level of the anus.

Transverse sections of the theca at various levels along the longitudinal axis of the aulacophore are probably not very dissimilar in

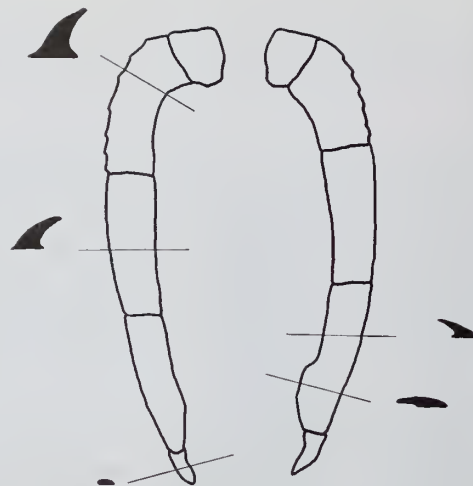


Fig. 3 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Cross-section of the marginalia at different levels along the thecal frame.

outline. Major morphological differences are due to the different curvature and width of the dorso-lateral projections of the marginalia, both of which decrease antero-posteriorly (Fig. 3).

VARIATION. Morphological differences between the most complete specimens of *Juliaecarpus* (see Table 1) as well as between isolated, homologous skeletal elements of its theca (especially marginalia, notably  $M'_1$ ) are negligible. Ontogenetic variation (if any) could not be detected, since the most complete individuals differ little in size and, therefore, their ontogenetic ages are assumed to be approximately the same.

Table 1 Estimated maximum thecal widths and lengths in some individuals of *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco.

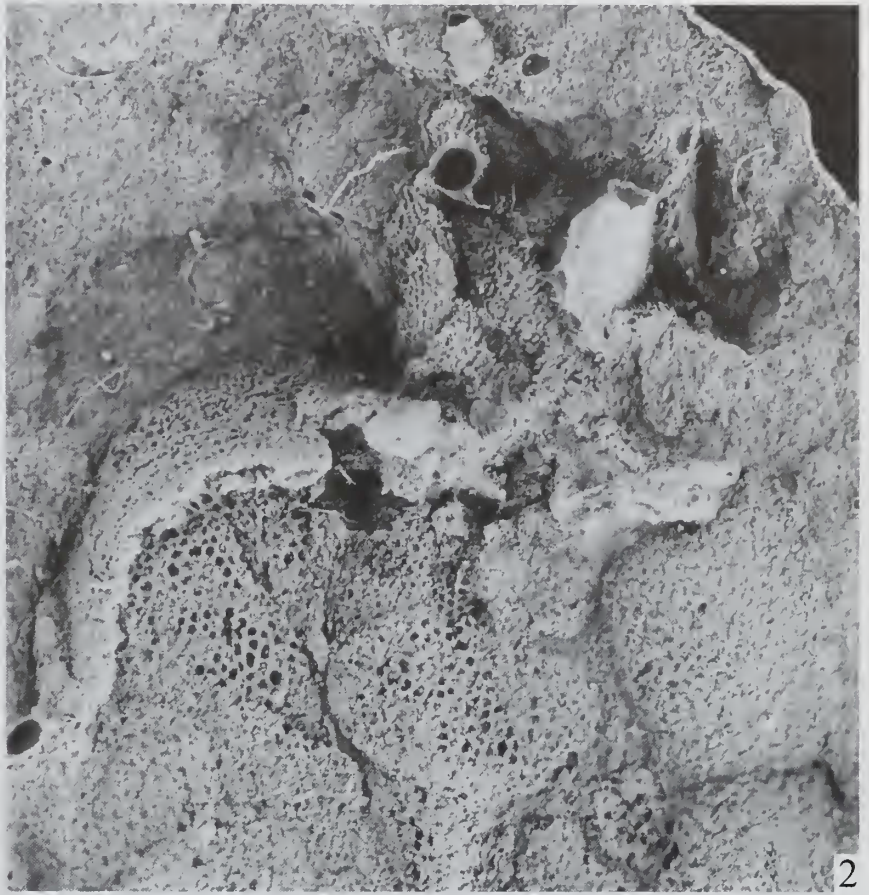
Specimen	Thecal length	Thecal width
BMNH EE 3069	10	6
BMNH EE 3070	7	4
BMNH EE 3072	9.5	5.5
BMNH EE 3083	9	5
BMNH EE 3101	10	5.5
BMNH EE 3119	7.5	4.5
BMNH EE 3121	10	6

Differences can be observed in the general outline of the theca (i.e. in its length/width ratio and in the degree of divergence of the lateral margins from the oro-anal axis in a posterior direction), in the curvature of  $M'_2$  and  $M_2$  in plan view, in the shape and curvature of the posterior zygial process of  $M'_1$  and of the posterior zygial plate, in the shape and arrangement of the supracentralia, in the more or less

## PLATE 1

*Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. 1, EE 3101,  $\times 9$ ; poorly preserved dorsal aspect of theca, aulacophore and obliquely oriented zygial bar. 2, EE 3072,  $\times 20$ ; arrangement of supracentralia on anterior half of theca and slightly disrupted aulacophore. 3, EE 3144,  $\times 10$ ; almost complete dorsal aspect of theca, arrangement of supracentralia and obliquely oriented zygial bar. 4, EE 3077,  $\times 8$ ; poorly preserved theca in dorsal aspect with well preserved aulacophore insertion. 5, EE 3119,  $\times 10$ ; well preserved theca in dorsal aspect showing almost undisrupted arrangement of supracentralia and suranal plate.







pronounced development of the peripheral flange and of the lateral thecal denticulations (both of which are normally reduced in size) and in the outline and relative size of the suranal plate.

Disruption and, occasionally, slight deformation of the fossil material are partially responsible for the observed variations of the thecal shape.

**MARGINAL PLATES.** The marginalia are divided into a group of five plates on the right side and a group of five plates on the left side of the theca. The rearmost left and right marginalia,  $M'_5$  and  $M_5$ , are scarcely visible, due to the generally poor preservation of the posterior part of the theca (see below).

The marginalia which occupy the same position in the left and right series with respect to the aulacophore insertion are not mirror images of each other. Rather, they show small but consistent differences in length and, to a much lesser extent, in shape. Each of the marginalia consists of a wider, dorso-lateral projection and a narrower, ventral projection. In cross-section, the dorso-lateral projections narrow slightly antero-posteriorly along the thecal frame and appear to be slightly wider than, and up to twice as wide as, the ventral projections, depending upon the position of the plate in the left or right marginal series. Conversely, the ventral projections are of almost uniform width throughout the left and the right series (e.g. Pl. 1, figs 3–5; Pl. 2, figs 1–5; Pl. 3, figs 1–5; Pl. 4, figs 1–2, 4–5). The dorso-lateral projections (Fig. 3) are gently to strongly convex in cross-section and slope ventralward and laterally, whereas the ventral projections are always flat. The convexity of the dorso-lateral projections is slightly more accentuated at the level of the antero-lateral angles of the theca and decreases rapidly in antero-posterior direction, so that at the level of its postero-lateral angles, the projections become almost flat (Pl. 1, figs 1–5; Pl. 2, figs 2, 4–5; Pl. 5, figs 1–2, 4; Pl. 7, figs 2, 4–6). The dorso-lateral and ventral projections of the marginalia meet at an acute angle forming a sharp lateral margin. Such an angle varies from about  $30^\circ$  in the most posterior portions of the thecal frame to about  $70^\circ$  at the level of its antero-lateral angles.

The thecal margins show a poorly developed flange (e.g. Pl. 1, figs 2–5; Pl. 2, figs 4–5; Pl. 7, fig. 2) characterized by a fibrillar stereom and restricted to the anterior half of the thecal frame.

The most anterior marginal plates,  $M'_1$  and  $M_1$ , contribute to the anterior thecal excavation for the aulacophore insertion (described in the next section). The space through which the internal cavity of the aulacophore communicates with the inside of the theca is roofed over by two adoral plates (see below) and delimited ventrally by the apophyses of  $M'_1$  and  $M_1$ . Given the complicated morphology of the internal (thecal) surface of  $M'_1$  and  $M_1$  and the fact that  $M'_1$  contributes to the zygial bar through its posterior process, both plates (including those parts of them which are visible from the outside in dorsal view, notably their dorso-lateral projections) will be described in detail in conjunction with the description of the internal aspect of the theca.

The asymmetries observed in the thecal frame are mainly due to the unequal size of  $M'_2$  and  $M_2$ , the length of the latter being approximately  $4/5$  the length of the former. Both plates are strongly curved medially in plan view and contribute to the lateral half of the right and left antero-lateral angles of the theca. Their dorso-lateral

projections are wider than those of more posterior marginalia. The dorso-lateral projection of  $M_2$  is of approximately constant width throughout the length of the plate and is slightly wider than the posterior half of the dorso-lateral projection of  $M'_2$ . The lateral margins of both plates bear poorly pronounced serrations with a gently sloping anterior surface and a steeply sloping posterior surface (Pl. 1, figs 2–4; Pl. 2, figs 1, 3, 5; Pl. 3, figs 1–5; Pl. 4, figs 1–2, 4–5; Pl. 5, figs 1–3; Pl. 7, fig. 2). The serrations result from the intersection of the lateral margins of  $M'_2$  and  $M_2$  with faint, transverse undulations visible on the lateral third of the dorso-lateral projections of these plates. The undulations become progressively shallower dorsalward before disappearing gradually. The serrations decrease slightly in size antero-posteriorly and disappear immediately posterior to the sutures between  $M'_2$  and  $M'_3$  and between  $M_2$  and  $M_3$ . The ventral projections of  $M'_2$  and  $M_2$  are of almost constant width, but widen slightly near their anterior ends and show characteristic embayments along their medial margins, marking a sudden change in their curvature (e.g. Pl. 2, fig. 1; Pl. 3, figs 1–5; Pl. 4, figs 1–2, 4–5).

$M'_3$  and  $M_3$  are shaped like elongate rods and are of approximately equal shape and size. Both plates are only gently convex laterally, their dorso-lateral projections show slightly concave to gently sinuous medial margins and their width decreases slowly antero-posteriorly. Their ventral projections possess broadly concave medial margins and are slightly narrower than their dorso-lateral projections. The medial margin of the ventral projection of  $M_3$  is often divided into a straight to gently concave posterior half and a more deeply concave anterior half (e.g. Pl. 2, fig. 1; Pl. 3, figs 1–2, 4; Pl. 4, figs 2–4).

$M'_4$  and  $M_4$  resemble  $M'_3$  and  $M_3$  in their elongate and rod-like aspect, but while  $M_4$  is either slightly shorter than or equal in length to  $M_3$ ,  $M'_4$  is always shorter than  $M'_3$ . Their dorsolateral projections are slightly narrower than those of more anterior marginalia throughout most of their length, but their posterior ends are expanded medially (especially in  $M_4$ ) to contact the suranal plate (see below). The lateral margins of  $M'_4$  and  $M_4$  are very gently convex. The ventral projection of  $M_4$  widens posteriorly sending a broadly triangular, medial spatulate flange in contact with the rearmost part of the posterior plate of the zygial bar along an antero-posteriorly elongate, straight suture. The flange forms a continuum with a similar, medially projected, subhorizontal and subrectangular flange of the dorso-lateral projection of  $M_3$ , thus interrupting posteriorly the trough-like internal surface of the plate (e.g. Pl. 1, figs 4–5; Pl. 2, figs 2–5; Pl. 5, fig. 2; Pl. 7, fig. 2; Pl. 8, fig. 3). The posterior ends of both  $M'_4$  and  $M_4$  are blunt, although their poor preservation does not permit their accurate reconstruction.

In some specimens, two small and irregular skeletal fragments with a characteristic reticulate stereom texture flank the suranal plate and are apparently loosely attached to the posterior ends of  $M'_4$  and  $M_4$  from which they are distinguished by the smaller width of their anterior half (e.g. Pl. 1, figs 4–5; Pl. 2, figs 2, 4; Pl. 7, figs 2, 4–5; Pl. 8, fig. 3). These fragments are interpreted as extremely reduced plates  $M'_5$  and  $M_5$ , loosely juxtaposed to the posterior half of the lateral margins of the suranal plate (see below). In some individuals (e.g. Pl. 2, fig. 4), the medial margins of  $M'_5$  and  $M_5$  seem to be slightly

## PLATE 2

*Juliacarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. **1**, EE 3079,  $\times 8$ ; incomplete theca in ventral aspect with poorly preserved infracentralia. **2**, EE 3129,  $\times 8$ ; almost complete theca in dorsal aspect with disrupted supracentralia. **3**, EE 3129,  $\times 8$ ; poorly preserved theca and aulacophore in ventral aspect, with faint impression of zygial bar and poorly preserved suranal plate. **4**, EE 3178,  $\times 20$ ; posterior half of theca in dorsal aspect, with well preserved suranal plate and posterior zygial plate in contact with right posterior part of thecal frame. **5**, EE 3072,  $\times 9$ ; almost complete but posteriorly disrupted theca in dorsal aspect.







bent towards the oro-anal axis and possess a blunt, rounded or plectrum-shaped posterior margin. In other specimens (e.g. Pl. 1, figs 4–5; Pl. 7, figs 2, 4–5),  $M'_5$  and  $M_5$  are vaguely rectangular or sub-semielliptical.

**ANTERIOR THECAL EXCAVATION.** The anterior thecal excavation occupies less than one quarter of the maximum thecal width and is formed mainly by the medially directed apophyses of  $M'_1$  and  $M_1$  and, in part, by the left and right adoralia (see below). The apophyses (Figs 2F, 6; Pl. 6, figs 1–3) are irregularly semielliptical to semicircular in outline and gently excavated both longitudinally and transversely. A shallow groove runs almost parallel to the dorsal margin of the upper half of each of the two apophyses, thus delimiting a smaller dorsal region from a slightly larger ventral region. A poorly defined, low ridge runs from the mid point of the medial margin of the apophysis to its centre just below the shallow groove. The ridge separates a deeper, medio-dorsal subtriangular area from a shallower, latero-ventral area.

The surface of each of the two apophyses slopes slightly forward near its ventral margin, but its upper half is almost vertical. Laterally, the apophyses merge smoothly into the ventral half of the dorso-lateral projections of  $M'_1$  and  $M_1$  (see description below) from which they are separated by a poorly pronounced, medially concave, crescent-shaped, blunt lateral margin.

**ADORALIA.** The left and right adoralia, LA and RA, occupy the most anterior part of the dorsal integument and roof over the anterior thecal excavation. Their preservation is invariably poor in the specimens examined and their margins are usually difficult to discern. In plan view, they are sometimes visible immediately posterior to the anterior thecal excavation (Fig. 2F–G; Pl. 1, figs 2–5; Pl. 2, figs 2, 5; Pl. 7, fig. 2). They are slightly smaller than the surrounding dorsal integument plates and RA is slightly larger than LA. Both plates vary in shape and size in different individuals, but this variation may be the result of disruption, at least in part. The presence of a right adoral orifice (a small opening piercing or notching RA; Ubahgs, 1968) cannot be detected. Despite the poor preservation, a median adoral is almost certainly absent.

Antero-laterally, each of the two adoralia is sutured with a triangular facet sitting on the antero-medial part of a wedge-like structure originating from the medial half of the dorso-lateral projections of  $M'_1$  and  $M_1$  (see description of these plates below).

LA is irregularly quadrangular to subpentagonal, slightly wider posteriorly than anteriorly and about half to two-thirds as large as RA. RA is usually longer than wide and subrectangular to subtrapezoidal in outline, generally with a broadly convex postero-lateral margin and with a gently concave medial margin accommodating LA.

Both adoralia possess a gently convex to flat dorsal surface. Partial collapse of these elements as a result of burial resulted in their lying slightly lower with respect to the dorsal margins of the dorso-lateral projections of  $M'_1$  and  $M_1$ . In life, LA and RA probably formed a gently arcuate structure bridging the space between the dorsal, antero-medial facets of  $M'_1$  and  $M_1$ , thus sitting immediately above the apophyses. The space comprised between the adoralia and the

apophyses was probably spindle-shaped to irregularly elliptical in life.

**ZYGAL.** The zygial (or zygial bar) runs obliquely from the left antero-lateral angle of the theca to the postero-lateral fourth of the right part of the thecal frame and is formed by a robust, posterior process of plate  $M'_1$  and by a posterior, elongate plate sutured with  $M_4$  and, perhaps,  $M_5$ . The ventral surface of the zygial is flat, whereas its dorsal surface is very gently convex and with a poorly pronounced subcentral keel (see below).

The length of the posterior zygial plate is about 5/7 the length of the posterior process of  $M'_1$ . The plate is at an angle of about 30° with the oro-anal axis and either forms a wide, obtuse angle with the  $M'_1$  process or is aligned with it. Its left and right margins are almost straight and diverge slightly antero-posteriorly. The average width of the plate is comparable with or slightly greater than that of the ventral projections of the marginalia. The posterior third of the plate is vaguely rectangular and spatulate and its left margin contacts the posterior end of  $M_4$  along a gently arcuate, longitudinal suture (Pl. 1, figs 1, 3–5; Pl. 2, figs 2, 4–5; Pl. 3, figs 1, 5; Pl. 4, fig. 1). The posterior margin of the posterior zygial plate is poorly preserved in the material observed and cannot be reconstructed with accuracy. It might have contacted the antero-medial angle of  $M_5$ , assuming the correct identification of this element (see above).

The process of  $M'_1$  (Pl. 1, figs 1–5; Pl. 2, figs 2, 4–5; Pl. 3, figs 1–2, 5; Pl. 4, figs 1, 5; Pl. 5, fig. 2; Pl. 6, figs 1–3; Pl. 7, figs 2–4; Pl. 8, fig. 3) is straight or, rarely, gently bent in its posterior half and lies slightly to the left of the oro-anal axis for most of its length, forming an angle of about 20°–25° with such an axis. The process is wider than the ventral projections of the marginalia, especially in its anterior two-thirds, and is about half as wide at its posterior end as at the level of the suture between  $M'_1$  and  $M_1$ . The lateral margins of the zygial process converge slightly posteriorly.

**DORSAL INTEGUMENT.** The supracentralia are mostly irregularly polygonal and sutured with each other along straight margins. Rarely they show gently curved margins. Some supracentralia, especially those situated along or in proximity to the oro-anal axis, are generally as wide as, or slightly wider than, the dorso-lateral projections of the marginalia. The supracentralia differ in shape and size, but most of them are roughly hexagonal or pentagonal. Rarely is their outline triangular or quadrangular. In at least one specimen (Pl. 3, fig. 4), the ventral surface of the dorsal integument is clearly visible.

Although no apparent distribution pattern is observed, the median and admedian supracentralia are on average larger than those sutured with the medial margins of the thecal frame. Generally, two subhexagonal supracentralia are distinguished from the others by their larger size and by the fact that they occupy a median position on the posterior half of the dorsal integument. Sometimes, a left and a right longitudinal row of three slightly smaller and subpentagonal plates flank the two subhexagonal supracentralia. Some of the supracentralia lying along the medial margins of the thecal frame are much longer than wide. The supracentralia which occupy the posterior half of the dorsal integument are usually of irregular shape and

### PLATE 3

*Juliacarpus milnerorum* gen. et sp. nov. Late Ordovician. Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. 1, EE 3070, × 9; almost complete ventral aspect of theca with slightly disrupted zygial bar; note styloid in right lateral view and poorly preserved ossicles. 2, EE 3144, × 10; incomplete ventral aspect of theca with disrupted zygial bar. 3, EE 3101, × 9; poorly preserved ventral aspect of theca, with almost complete proximal aulacophore, well preserved styloid and proximal ossicles. 4, EE 3121, × 8; internal aspect of dorsal side of theca, heavily disrupted along the posterior half of its right margin; note the internal, trough-like aspect of the marginalia. 5, EE 3072, × 9; almost complete ventral aspect of theca; note robust posterior zygial plate.







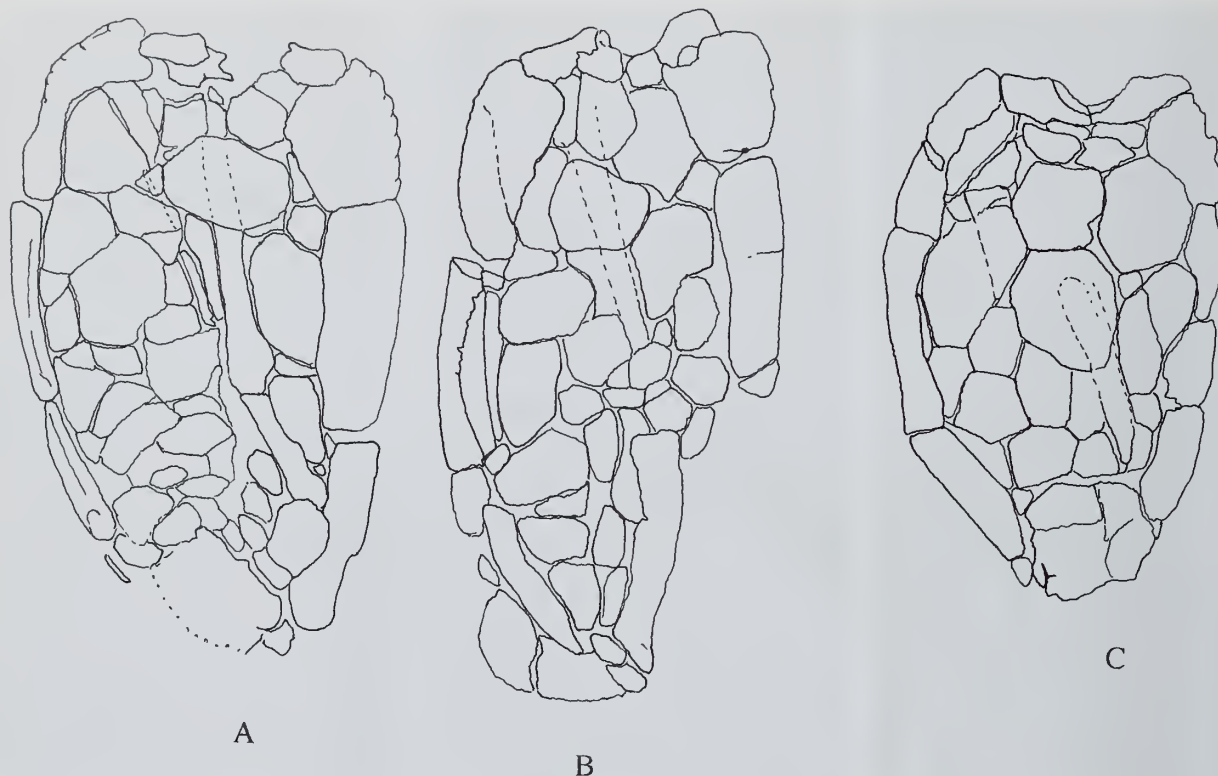


Fig. 4 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Camera lucida sketches of outline of supracentralia in different individuals. A, EE 3072,  $\times 6$ . B, EE 3144,  $\times 7$ . C, EE 3119,  $\times 7$ .

subequal size (Fig. 4; Pl. 1, figs 2–5; Pl. 2, figs 2, 4–5; Pl. 3, figs 2, 4; Pl. 5, figs 1–2; Pl. 7, fig. 2, 4–5; Pl. 8, fig. 3).

A large suranal plate (Figs 1–2, 5; Pl. 1, fig. 5; Pl. 2, figs 4–5, 4; Pl. 3, fig. 4; Pl. 4, fig. 5; Pl. 5, figs 1–2; Pl. 7, figs 2, 4; Pl. 8, fig. 3), sloping slightly ventralward towards its posterior margin, is present between the rearmost margins of  $M'_4$  and  $M_4$ . Its posterior margin roofs over the anal opening. In some specimens, the suranal is broadly trapezoidal in outline. In others, it is rectangular or, rarely, roughly elliptical. Although the suranal is variable in shape, it is always possible to distinguish four margins: a straight to gently sinuous anterior margin loosely articulated with a variable number of posterior supracentralia; two irregularly sinuous lateral margins in contact along their posterior half with the medial margins of  $M'_5$  and  $M_5$  and along their anterior half with the rearmost part of the medial margins of  $M'_4$  and  $M_4$ ; and a broadly convex, posterior margin with a variable degree of curvature and usually displaying a well developed fringe (see description of stereom below). The posterior margin is usually very slightly offset with respect to the position of the oro-anal axis. The dorsal surface of the suranal plate is flat to very gently

convex in its central part and flat along its posterior margin and slopes gently ventralward near its lateral margins.

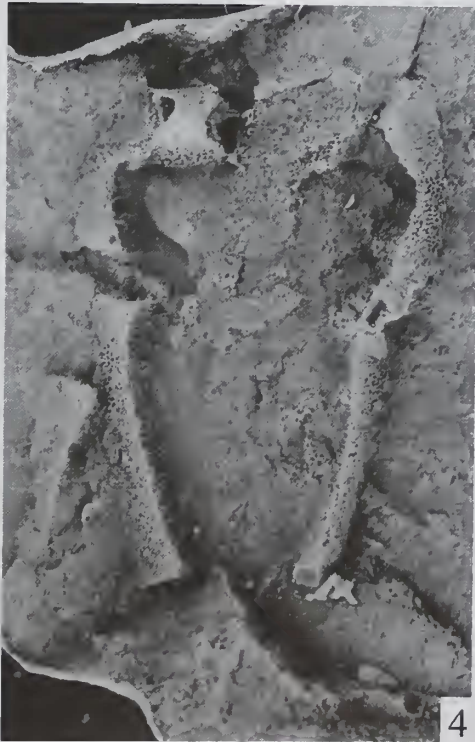
**VENTRAL INTEGUMENT.** The ventral integument (Pl. 2, figs 1, 3; Pl. 3, figs 1, 3, 5; Pl. 4, figs 1–2, 4) is flat and divided by the zygial bar into two antero-posteriorly elongate areas of slightly different size, the left area being slightly broader than the right area. The infracentralia are generally more poorly preserved than the supracentralia, but seem to have been more irregular in outline and of various shapes and sizes. As in the case of the supracentralia, they do not seem to have been imbricated or to have shown a regular arrangement, but their boundaries are difficult to delimit.

Unfortunately, in none of the specimens of *Juliaecarpus* is the ventral integument complete and its posterior part is invariably damaged or missing. Therefore, the reconstruction of the infracentralia which floor the anal opening is only tentative and it is impossible to say whether the ventral margin of the anus was bordered by flexibly articulated, narrow, elongate platelets arranged in a fan-like pattern (as in the case of the ankyroid *Amygdalotheca*

#### PLATE 4

*Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. 1, EE 3069,  $\times 10$ ; heavily disrupted theca in ventral aspect; note shape and proportions of posterior zygial process. 2, EE 3115,  $\times 10$ ; incomplete and laterally compressed theca in ventral aspect. 3, EE 3181,  $\times 15$ ; isolated marginal element in internal view, possibly  $M_4$ . 4, EE 3162,  $\times 10$ ; incomplete and disrupted theca in ventral aspect. 5, EE 3162,  $\times 10$ ; posteriorly disrupted theca in dorsal aspect with partially preserved supracentralia.





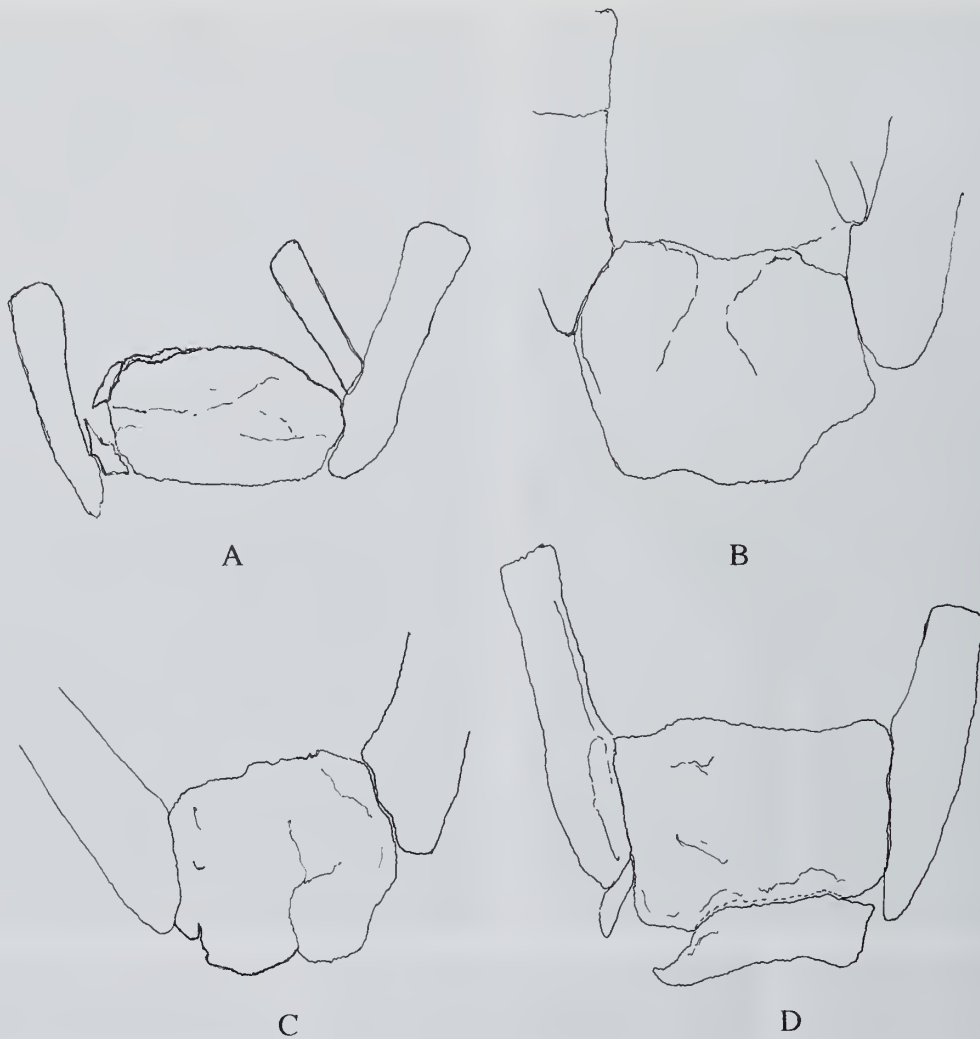


Fig. 5 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Camera lucida sketches of outline of suranal plate in different individuals. A, EE 3184,  $\times 7.5$ . B, EE 3178,  $\times 13$ . C, EE 3119,  $\times 13$ . D, EE 3121,  $\times 7.5$  (seen from the inside).

*griffei* Ubaghs, 1969) or by a mosaic of relatively large, polygonal elements (as in *Reticulocarpus hanusi* Jefferies & Prokop, 1972).

**INTERNAL ASPECT OF THE THECA.** The internal surfaces of both the supracentralia and the infracentralia are featureless. The surface of the marginalia facing towards the inside of the theca is trough-like (Fig. 3; Pl. 3, figs 1–5; Pl. 4, figs 1–4). Its cross-section does not show abrupt changes in curvature, but it varies considerably in depth depending upon the relative width of the dorso-lateral and ventral projections of the marginalia. Thus, at the level of the antero-lateral angles of the theca, the surface is approximately semiparabolic to semicircular in cross-section, whereas halfway along the length of

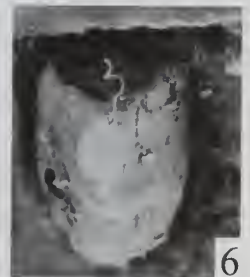
the lateral thecal margins, its section is semielliptical. It becomes shallower and broadly hyperbolic at the level of the postero-lateral angles of the theca.

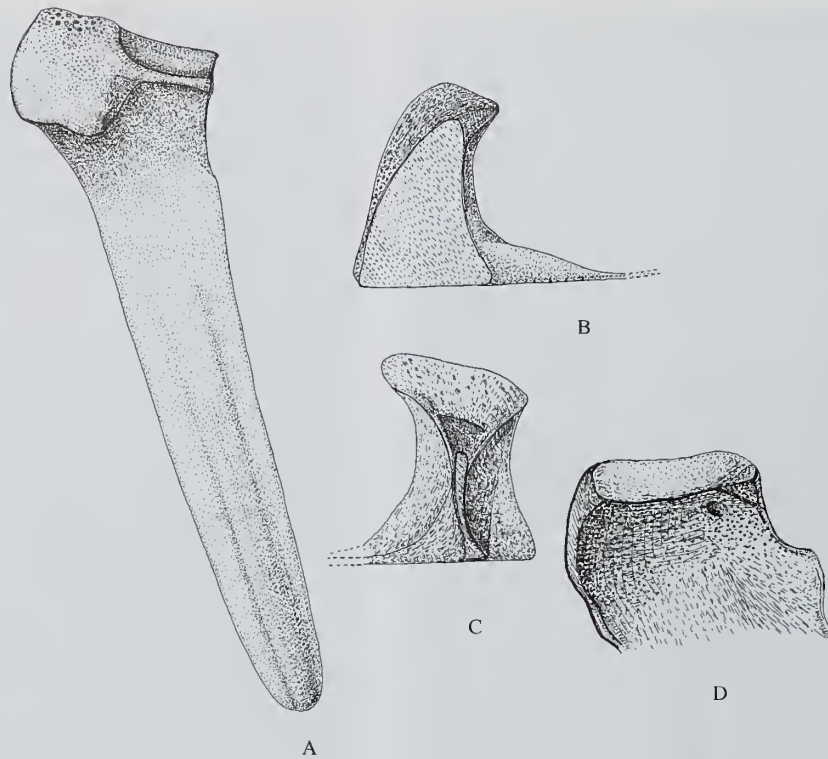
The internal surfaces of plates  $M'_1$  and  $M_1$  and of the zygial bar show a complex morphology. In fully articulated specimens of *Juliaecarpus*, the dorso-lateral projections of  $M'_1$  and  $M_1$  are largely visible in dorsal view. They contribute laterally to the medial parts of the antero-lateral angles of the theca and project medially into the apophyses for the aulacophore insertion (see above).  $M'_1$  and  $M_1$  do not differ remarkably from each other except for the presence of a posteriorly directed process contributing to the zygial bar in  $M'_1$ . In what follows, therefore, I shall

#### PLATE 5

*Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. 1, EE 3115,  $\times 10$ ; laterally compressed and disrupted theca in dorsal aspect, with displaced supracentralia and poorly preserved styloid and ossicles. 2, EE 3069,  $\times 10$ ; almost complete theca in dorsal aspect, with slightly displaced marginalia and supracentralia; note disrupted plates of proximal aulacophore. 3, EE 3071,  $\times 15$ ; isolated proximal aulacophore plates, ossicles, cover plates and proximal-most portion of theca in dorsal aspect. 4, EE 3098,  $\times 10$ ; poorly preserved marginalia and styloid articulated with first ossicle in left lateral view. 5, EE 3157,  $\times 15$ ; isolated plate  $M_2$  in dorsal aspect. 6, EE 3151,  $\times 15$ ; poorly preserved styloid with broken anterior spike in ventral aspect.







**Fig. 6** *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Reconstruction of plate  $M'_1$  and of its zygial process. **A**, dorsal aspect. **B**, left lateral aspect of most anterior part. **C**, right lateral aspect of most anterior part. **D**, internal aspect of most anterior part (rear end of plate slightly tilted dorsally).

describe in detail only the internal surface of  $M'_1$  including its zygial process (Fig. 6).

In ventral view, the boundary between  $M'_1$  and its posterior process corresponds to a hypothetical, oblique line connecting the posterior end of the suture between  $M'_1$  and  $M_1$  with the posterior end of the suture between  $M'_1$  and  $M'_2$ . On the internal surface of  $M'_1$ , this line delimits the posterior boundary of a flat, subrectangular region sloping slightly dorsalward both anteriorly and medio-laterally. The anterior boundary of this region is represented by a poorly pronounced crest with a broadly concave dorsal margin. Such a crest forms the dorso-medial margin of the left apophysis. It becomes less pronounced and flatter laterally, where it widens to form a blunt-topped, crescentic ridge separating the apophysis from the dorso-lateral projection of  $M'_1$ .

The dorso-lateral projection of  $M'_1$  (Pl. 6, figs 1–3) has a broadly trapezoidal outline and is gently convex both longitudinally and, to a lesser extent, transversely. Its ventral half is almost vertical and bends sharply rearward to continue into the ventral surface of the plate. The dorso-lateral projection of  $M'_1$  bends abruptly rearward at the level of the medial half of its dorsal margin giving rise to a stout,

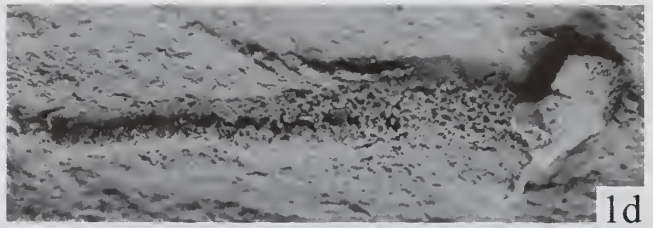
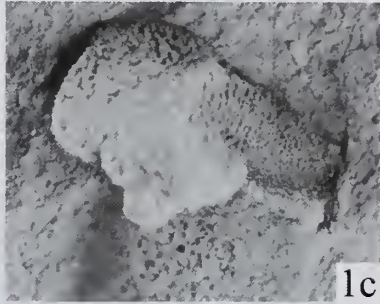
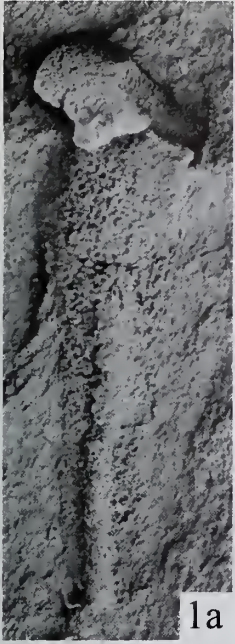
dorsal wedge-like structure, slightly thicker medially than laterally and bearing a flat, tongue-shaped posterior process. The dorsal surface of this process slopes slightly downward both in a rearward direction and in a medio-lateral direction. The antero-medial part of the wedge-like structure is truncated, triangular in outline and flat-surfaced, and articulated with the left adoral plate (see above). The ventral apex of this articular surface contacts the lateral end of the crest-like, dorso-medial margin of the left apophysis. The postero-medial surface of the tongue-shaped posterior process is beak-like in outline and deeply excavated, whereas its postero-lateral surface is comparatively less expanded dorso-ventrally, less arcuate in plan view and convex outward. Its medial half slopes upward laterally and continues into the almost horizontal lateral half. Both surfaces merge ventrally into the trough-like thecal surface of the plate, which continues posteriorly into the dorsal surface of the zygial process.

The dorsal surface of the zygial process (Fig. 6; Pl. 6, figs 1–3) is flat or very gently convex in transverse section in its anterior quarter. The posterior three-quarters of it is occupied by a straight ridge which is slightly closer to the right margin of the zygial process than it is to its left margin. The ridge is wider and less pronounced in its

#### PLATE 6

*Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. 1, EE 3143; **a**, **d**,  $\times 12$ ; **b**, **c**,  $\times 20$ ; dorsal aspect of plate  $M'_1$ ; note dorso-lateral projection and apophysis of plate, and internal ridge on its dorsal surface. 2, EE 3101,  $\times 20$ ; internal ridge on dorsal surface of  $M'_1$ . 3, EE 3117; **a**,  $\times 20$ ; **b**,  $\times 10$ ; dorsal aspect of  $M'_1$ .







anterior half than in its posterior half. Anteriorly, it appears to be very slightly raised above the level of the internal surface of the zygial process. Posteriorly, it becomes almost semicylindrical in shape. The transition between the anterior half and the posterior half is nearly abrupt. The anterior end of the ridge merges gradually into the internal surface of the zygial process.

**STEREOM.** Unlike the marginalia, all integument plates are made of a 2-dimensional stereomic meshwork, consisting of regularly arranged, subcircular to subhexagonal pores separated by short trabeculae. The stereom fabric of the marginalia differs slightly from that of the dorsal and ventral integuments. In addition, the texture of the peripheral margin is more irregular than that of the remaining surface area of the marginalia.

There are indications that the suranal plate likewise consisted of a 2-dimensional meshwork, at least peripherally. However, the central part of this plate may have been formed by a 3-dimensional meshwork, albeit considerably less thick than the marginalia (e.g. Pl. 2, fig. 4). The stereom of the suranal plate is most characteristic in that it changes remarkably from the centre towards the periphery of the plate. The stereom texture of a roughly bell-shaped area of the external surface of the suranal plate comprised between its centre and its anterior margin is of the reticulate type observed in the supracentralia and infracentralia, although the size of the holes is on average slightly larger than in the integument plates. The size of the holes becomes progressively smaller towards the lateral margins and the antero-lateral angles of the plate, where the trabeculae are thicker and shorter than in its central part. The smallest size of the holes is observed at the level of a broadly crescentic area lying immediately anterior to the posterior margin of the plate, where the trabeculae seem to be flat-topped. Trabeculae and holes become more irregular, antero-posteriorly elongate and arranged according to a broadly fringe-like pattern along the posterior margin of the suranal plate. The fringe extends slightly posterior to the rearmost ends of the left and right parts of the thecal frame and consists of narrow, finger-shaped trabeculae of approximately equal length separated by elongate holes of variable length and outline. Rarely are adjacent trabeculae connected by thin, transverse rods or walls. The rearmost ends of the trabeculae are extremely variable in shape (spatulate, pointed or rounded), so that the fringe appears to have an irregular outline. The lateral ends of the fringe consist of remarkably short trabeculae with rare intercalated holes, and pass abruptly into the postero-lateral angles of the suranal plate.

The texture of the internal and external surface of both the supracentralia (Pl. 1, figs 2–5; Pl. 2, figs 2–4, 5; Pl. 3, figs 2, 4; Pl. 5, figs 1–2; Pl. 7, fig. 2, 4–5; Pl. 8, fig. 3) and the infracentralia (Pl. 2, figs 1, 3; Pl. 3, figs 1, 3, 5; Pl. 4, figs 1–2, 4) does not change remarkably, although in the case of the supracentralia, their internal surfaces show smaller, more irregular and more widely spaced pores than their external surface.

Changes in the stereom texture of the marginalia are best described by reference to the illustrations (e.g. Pl. 1, figs 2–5; Pl. 2, figs 4–5; Pl. 3, fig. 3; Pl. 6, figs 1–3; Pl. 7, fig. 2; Pl. 8, figs 1–2). I only point out that the most remarkable feature of the stereom of the inside

of the marginalia is the transverse elongation of some pores in the deepest portions of the trough-like internal excavations of the plates (e.g. Pl. 4, fig. 3).

## Aulacophore

**PROXIMAL PART.** The proximal part of the aulacophore is invariably disrupted or missing in the material studied (Pl. 1, fig. 2; Pl. 2, fig. 5; Pl. 3, figs 1, 3, 5; Pl. 5, figs 1–3; Pl. 7, figs 2, 6; Pl. 8, figs 1–2). Tectals and inferolaterals are likely to have formed two dorsal and two ventral longitudinal rows respectively, although their precise arrangement cannot be reconstructed accurately. In few specimens (e.g. Pl. 7, fig. 2), it is possible to observe three to four small segments aligned longitudinally despite the extensive disruption and partly overlapping each other, although the latter condition may represent an artifact of preservation rather than a genuine feature.

Some of the plates of the proximal aulacophore are strongly arcuate in transverse section and approximately square in outline. One of their two longest margins is gently convex whereas the other margin is slightly concave. The two shortest margins of the plates in question differ in length and shape; the shorter of these margins is straight, whereas the longer one is broadly concave and projects into a small conical process at one of its extremities.

By comparison with the proximal part of the aulacophore of *Reticulocarpus hanusi*, as reconstructed by Jefferies & Prokop (1972), I suggest that the arcuate plates in question may belong to the longitudinal ventral series and, therefore, may correspond to inferolaterals. If this interpretation is correct, the conical processes would occupy the ventral, antero-lateral angles of the arcuate plates, following the anatomical orientation adopted in this paper.

Another kind of plate is represented by slightly arcuate elements without conical projections and rectangular in outline (e.g. Pl. 1, fig. 2). These may belong to the longitudinal dorsal series and may thus correspond to tectals. As in *Reticulocarpus*, the plates of the proximal part of the aulacophore probably decreased in size to a small extent anteriorly. This is suggested by the fact that the posterior part of the styloid of *Juliaecarpus*, around which the most anterior tectals and inferolaterals were probably wrapped up in life, is just smaller than the thecal excavation for the aulacophore insertion.

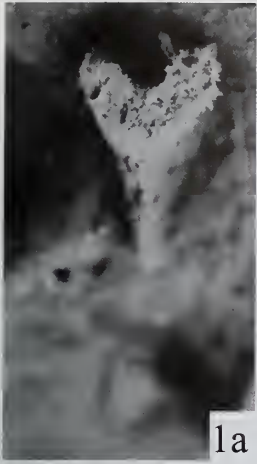
It is impossible to say whether these two kinds of plates were sutured along their lateral and medial margins to form complete tetramerous rings or whether elements of the dorsal and/or the ventral longitudinal series were separate. Likewise, it is impossible to ascertain whether the plates formed opposite or alternate rows dorsally and/or ventrally. The presence of small intercalary plates, reported by Jefferies & Prokop (1972) in the proximal part of the aulacophore of *Reticulocarpus*, is difficult to document in *Juliaecarpus*. Small, subrhomboidal elements found in some specimens in the region of the proximal aulacophore may represent intercalary plates or fragments of tectals and inferolaterals (e.g. Pl. 5, figs 1–2).

**INTERMEDIATE PART.** The styloid is a robust structure, slightly longer than wide, consisting of a saddle-shaped posterior part and a

## PLATE 7

*Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. **1a, b**, EE 3175, × 20; posterior aspect of isolated ossicle; note changes in stereom structure along the spike. **2**, EE 3070, × 15; complete but slightly flattened theca in dorsal aspect with poorly preserved aulacophore; note dorso-lateral projections of M<sub>1</sub>' and M<sub>1</sub>. **3**, EE 3141, × 10; incomplete and heavily disrupted theca in dorsal aspect; note massive aspect of posterior zygial process in the centre of the photograph. **4**, EE 3184, × 5; incomplete and slightly disrupted theca in dorsal aspect; note well-preserved and articulated supracentralia, and disrupted zygial bar. **5**, EE 3152, × 6; poorly preserved theca in ventral aspect with damaged and displaced infracentralia. **6**, EE 3146, × 10; poorly preserved aulacophore in right lateral view, with complete styloid and broken first ossicle articulated with it.





1a



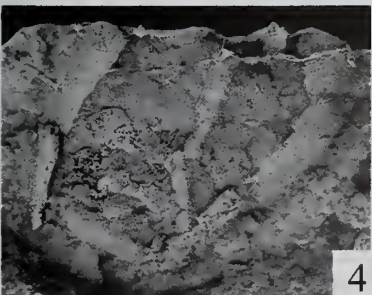
1b



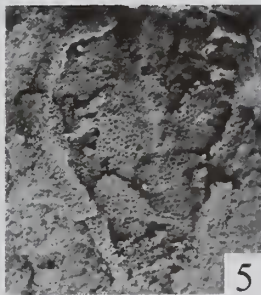
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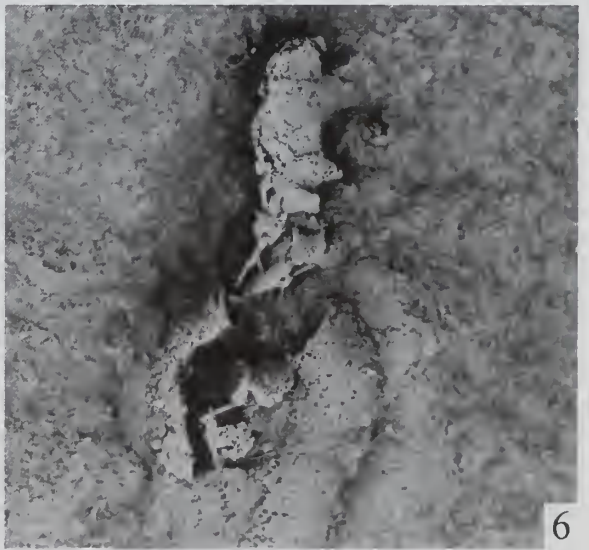
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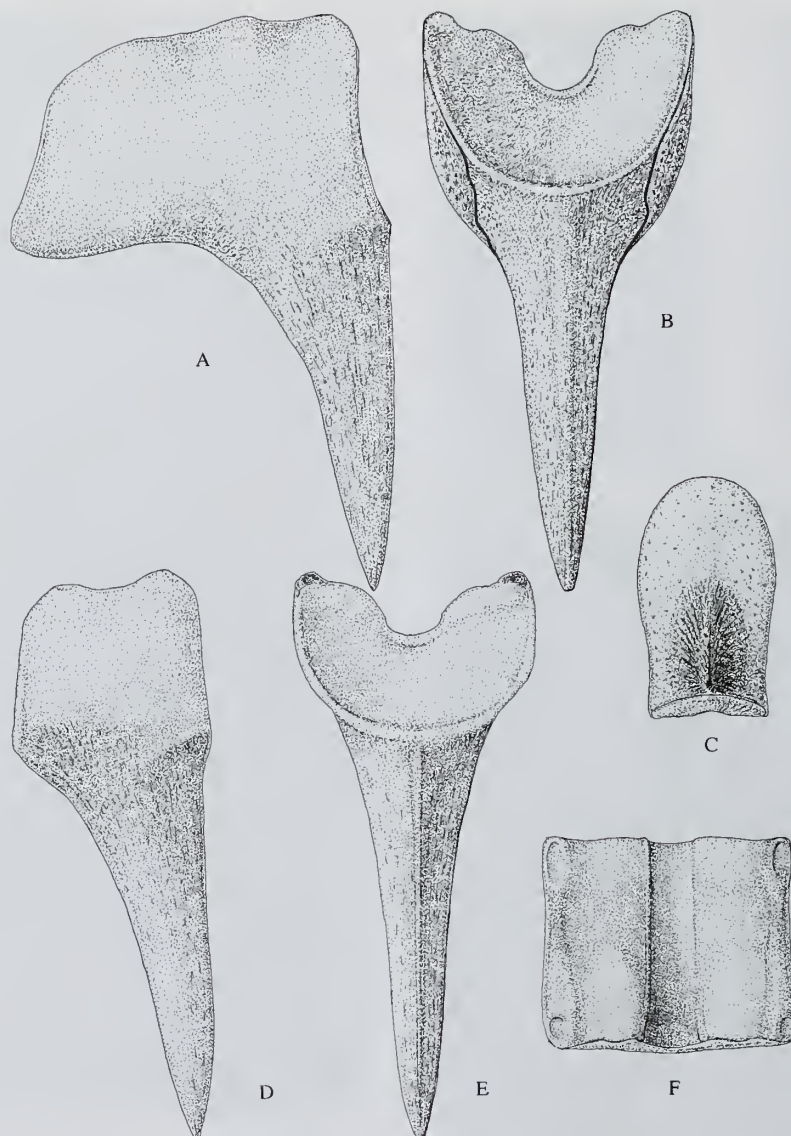
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5



6



**Fig. 7** *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Reconstruction of external and internal aspects of styloid and of a proximal ossicle. **A**, right lateral view of styloid. **B**, anterior view of styloid. **C**, ventral view of styloid (much reduced with respect to A and B). **D**, right lateral view of ossicle. **E**, posterior view of ossicle. **F**, dorsal view of ossicle.

well developed anterior spike (Fig. 7A–C; Pl. 2, fig. 3; Pl. 3, figs 1, 3–4; Pl. 5, figs 1, 3–4; Pl. 7, fig. 6; Pl. 8, figs 1–2). The posterior part is gently arcuate ventrally in lateral view and is about as long as wide. Its ventral surface is approximately semicircular in cross-section. Its lateral surfaces are subparallel and slightly convex to flat in their uppermost part and decrease rapidly in height posteriorly converg-

ing into a broadly semicircular posterior margin. The latter forms the postero-ventral boundary of a circular excavation which occupies the posterior half of the styloid. The excavation lies on an oblique plane oriented at an acute angle with the horizontal plane.

The height of the spike is slightly greater than the total length of the styloid. The spike is gently curved backward near its apex,

#### PLATE 8

*Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. **1**, EE 3101,  $\times 20$ ; close-up of aulacophore; note partly damaged styloid spike. **2**, EE 3070,  $\times 20$ ; posterior half of ventral aspect of theca and poorly preserved styloid and ossicles. **3**, EE 3178,  $\times 8$ ; almost complete, slightly compressed theca of an individual in dorsal aspect (bottom end of photograph), poorly preserved theca of a second individual in dorsal aspect (centre) and isolated plate M'<sub>3</sub>.







slightly compressed laterally, with blunt anterior and posterior margins, elliptical in cross-section throughout most of its height and roughly circular near its apex. Its lateral surfaces are gently concave in the upper two-thirds and merge smoothly into the posterior part of the styloid. Its posterior margin meets the posterior part of the styloid along a smooth, hyperbolic curve in lateral view.

**DISTAL PART.** Isolated ossicles and paired plates are observed in some specimens (Fig. 7D–F; Pl. 2, fig. 3; Pl. 3, figs 1, 3, 5; Pl. 5, figs 3–4, 6; Pl. 7, figs 1, 6; Pl. 8, figs 1–2). In a few individuals, the distal part of the aulacophore is preserved articulated and straight and consists of two or three segments. However, it is not absolutely certain that a short distal aulacophore represents a genuine feature of *Juliaecarpus*. Jefferies & Prokop (1972) argued in favour of the presence of a reduced distal aulacophore (their hind tail) in *Reticulocarpos hanusi* (see also below). Although it is possible that the aulacophores of both *Reticulocarpos* and *Juliaecarpus* consisted of a greatly reduced number of segments in comparison with those of other stylophorans, it is risky to deduce their original length from the available material.

As noted by Lefebvre *et al.* (1998), the distal part of the stylophoran aulacophore is extremely fragile and often incompletely preserved. In addition, because the distal aulacophores of both *Reticulocarpos* and *Juliaecarpus* seem to have been rigid, it is likely that they broke up rather easily during diagenesis or burial and that its various segments were dragged away from the rest of the body. It is possible, therefore, that more distal ossicles were present in life.

As in the case of the styloid, each ossicle consists of an upper, massive part and a lower, recurved spike. The massive part is just wider than long and composed of anterior and posterior articular surfaces, two lateral surfaces and an upper surface. The anterior and posterior articular surfaces are subequal in shape and size and roughly crescentic. The posterior surface is flat except for the presence of a poorly developed ridge occupying the central third of its lower margin. The anterior surface is slightly depressed in its lower half and shows no ridges. The lower margins of both the anterior and the posterior surfaces are accurately semicircular. Their upper margins are complicated by the intersection of both articular surfaces with the system of longitudinal grooves and thickenings present on the upper surface of the massive part. The lateral surfaces of the massive part are very gently convex in transverse section and broadly rectangular in outline, and diverge slightly lateralward in dorsal direction. They merge gradually into the lateral surfaces of the spike from which they are separated by a very low, almost indistinct subhorizontal ridge disappearing rapidly anteriorly. The upper surface of the massive part is deeply concave and carries a median longitudinal furrow (Ubaghs, 1968) with a broadly parabolic cross-section. The furrow is flanked by a left and a right thickening, about half as wide as the groove and with a blunt, gently convex top. The thickenings are asymmetrical in cross-section, for they slope slightly upward in a medio-lateral direction. The most lateral parts of the upper surface are generally poorly preserved. However, it is possible to see the presence of left and right bump-like projections about half as long as the ossicles and slightly displaced anteriorly. Immediately posterior to these projections are very shallow, straight transverse channels, slightly diverging posteriorly from the median longitudinal furrow and apparently intersecting the lateral thickenings.

The ossicular spike is almost twice as high as the massive part and laterally compressed for most of its height, so that its cross-section appears to be subelliptical. Near its apex, the spike is more rounded in section and ends in a subconical point. The anterior and posterior margins of the spike are narrowly acute in section, although never acutely sharp, and concave in lateral profile, the posterior margin

more so than the anterior margin. In lateral view, the uppermost part of the posterior margin forms a small angle with the posterior articular surface of the massive part. As a result, the spike points almost exactly ventralward rather than posteriorly as in *Reticulocarpos*. In their upper third, the lateral surfaces of the spike are gently concave, whereas at the level of their lower third they are mostly flat and subparallel. The distance between the anterior and the posterior margin of the spike decreases rapidly dorso-ventrally.

The paired plates of the distal aulacophore are not preserved in place. However, I interpret as disarticulated plates several small, subcircular to plectrum-shaped elements with a characteristic radial striation pattern. These are visible in proximity to the ossicles in some specimens (e.g. Pl. 8, fig. 1). The margin of the plates towards which the striae radiate out may correspond to their anterior side, although this is not certain.

**STEREOM.** The plates of the proximal part of the aulacophore display a retiform stereom similar to that of the centralia and marginalia, although the average size of the perforations is much smaller. The perforations are apparently distributed regularly on the surface of the plates. Those plates which are here interpreted as inferolaterals show a radiating pattern of trabeculae separated by elongate pores in their posterior half.

The stereom texture of the ossicles (Pl. 5, fig. 3; Pl. 7, fig. 1; Pl. 8, fig. 1) differs in the massive part and along the height of the spike. As far as the massive part is concerned, its anterior, posterior and upper surfaces, as well as the upper parts of its lateral surfaces, show a compact stereom, with no apparent texture pattern. The stereom texture is reticulate at the level of the upper half of the lateral surfaces of the spike, whereas its anterior and posterior margins and the apex show an irregularly perforated to coarsely granular texture consisting of short trabeculae and shallow pits. The stereom of the paired plates is mostly reticulate, but becomes compact or granular along their margins.

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## FUNCTIONAL MORPHOLOGY

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### General considerations

**INTRODUCTION.** Despite several claims to the contrary (e.g. Jefferies, 1984, 1986 and references therein), a consensus on the functional morphology of the stylophorans (or on any other aspect of their palaeobiology) has not yet been reached (Ruta, 1998, in press). Although some inferences are plausible (e.g. Jefferies & Prokop, 1972; Daley, 1992; Woods & Jefferies, 1992; Donovan, in press), they do not necessarily imply the correctness of the life-style interpretations proposed for these animals. Ubaghs (1968) provided the most comprehensive summary of the various functional hypotheses put forward so far (see also Ubaghs, 1981; Jefferies, 1986 and Kolata *et al.*, 1991).

In this section, the functional adaptations of the theca (including its dorsal and ventral integuments) and suranal plate of *Juliaecarpus* are analyzed and the significance of certain anatomical features (especially the lateral profile of the theca) in relation to the stability of the animal in water currents is examined in detail.

A brief account of the possible functions of the aulacophore (feeding organ; locomotory device) is dealt with in the next two sections and a reconstruction of the locomotory cycle of *Juliaecarpus* is presented.

**FUNCTIONAL ADAPTATIONS OF THE THECA.** Before discussing the external anatomy of *Juliaecarpus* from a functional viewpoint, it is necessary to consider briefly the ankyroid *Reticulocarpos hanusi*,



the biomechanics and locomotion of which were analyzed in great detail by Jefferies & Prokop (1972). It is reasonable to apply some of Jefferies & Prokop's (1972) arguments also to *Juliaecarpus*, given the fundamental anatomical resemblance between the latter and *Reticulocarpus* (see also the section on morphological comparisons below).

According to Jefferies & Prokop (1972), *Reticulocarpus* was fundamentally adapted to staying up on a soft sea-bottom, aided in this by the weight-bearing capacity of the muddy substrate rather than by compensation through lateral displacement of the sediment (see also Jefferies, 1975, 1981 for a discussions of the biomechanical constraints imposed by the two methods in different stylophorans). The following morphological features of *Reticulocarpus* suggest such a life-style: 1) flat ventral surface of the theca; 2) nearly bilaterally symmetrical outline; 3) perforated texture of the stereom; 4) presence of a peripheral flange; 5) small size. Jefferies & Prokop (1972) considered these features to be adaptations for reduction of the total skeletal mass of the animal, reduction of its weight per unit area and even distribution of the body weight to the sediment through the flat ventral side of the theca.

The fact that the thecal outline of *Juliaecarpus* is more bilaterally symmetrical than that of *Reticulocarpus* implies that in *Juliaecarpus*, the thecal weight may have been distributed to the sediment more uniformly than in *Reticulocarpus* and in approximately equal amounts on the left and on the right sides of the theca with respect to the oro-anal axis. A more bilaterally symmetrical outline may also have involved greater stability in the water currents and a more effective manoeuvrability of the theca during locomotion, when the animal pulled itself along dragged by its aulacophore (see below for a reconstruction of the locomotion in *Juliaecarpus*).

The lateral profile of the theca of *Juliaecarpus*, as reconstructed in this paper, appears to be very low and decreases progressively in height from the aulacophore insertion to the anal opening (see anatomical description above). In addition, neither the supracentralia nor the marginalia show projections or irregularities of any sort. With a certain approximation, such a low, almost smooth lateral profile is similar to the cross-section of a hydrofoil.

This observation suggests that, perhaps, water turbulence was drastically reduced or even absent all around the theca of *Juliaecarpus*. A regularly laminar, or almost laminar, water flow may have contributed to stabilize the animal in a regime of currents, perhaps supplementing the anchoring action of its styloid and ossicular spikes (see below). Slowing down of the flow at the level of the theca/aulacophore junction (where the theca reached maximum thickness) or even production of eddies immediately above this region may have resulted in a slight increase in the fluid pressure (Bernoulli effect), thus preventing forces generated by the water currents from lifting the theca off the sea-floor. A similar hydrodynamic mechanism counteracting the action of currents, based on a series of flume tank experiments, was proposed by Daley (1996) for the North American Middle Cambrian solute *Coleicarpus sprinklei*.

The smaller size of the lateral denticulations of  $M_2^1$  and  $M_2$  of *Juliaecarpus* with respect to those of *Reticulocarpus* and the less developed peripheral flange may have represented further adaptations to weight reduction, although this conclusion is not certain.

Stability in water currents, especially when *Juliaecarpus* was at rest on the sea bottom, was perhaps achieved in part through the suction forces acting along the flat, ventral surface of the theca. Suction forces, although not hampering the movements of the animal along the sea bottom, probably prevented its theca from tilting (see below). It is possible that, as in the case of other cornutes (e.g. see Daley, 1992), the zygial bar of *Juliaecarpus* may have helped reduce suction forces during the lateral power strokes of the aulacophore

(see reconstruction of the locomotory cycle below), presumably by interrupting the continuity of the smooth, ventral integument.

Thus, it is proposed that suction forces may have played an important role in stabilizing the animal in water currents, acting along the flat, ventral projections of the marginalia. At the same time, however, such forces had to be reduced in part when the animal pulled itself along the sea-floor. Reduction may have occurred essentially along a direction following the course of the zygial bar and was most important at its anterior end, near the theca/aulacophore insertion, where forces exerted by the lateral pushing movements of the aulacophore were transmitted to the theca.

**INTEGUMENTS.** It is not clear to what extent the dorsal and ventral integuments of *Juliaecarpus* were flexible in life. The occurrence of broad, almost polygonal plates that did not overlap each other (especially on the dorsal integument) certainly accounts for reduced flexibility. The integument is remarkably different from that of certain primitive cornutes (e.g. several boot-shaped forms), in some of which it consisted largely or exclusively of small, round or subpolygonal elements, presumably partly embedded in a soft tissue and not abutting against each other. Some degree of flexibility may have developed along the peripheral margins of the dorsal and ventral integuments of *Juliaecarpus* and in the portion of the dorsal integument lying immediately anterior to the suranal plate.

However, compression or expansion of the integuments was perhaps limited by the constructional morphology of the supracentralia and infracentralia. In fact, flexibility may have been limited to restricted portions of the integuments (e.g. the periproctal region or the integumental periphery) in most if not all ankyroids. In these, the integument plates usually grew larger than in the asymmetrical cornutes and, in some cases (e.g. Cripps, 1989a; Ubaghs, 1991; Cripps & Daley, 1994), the integuments consisted of few, large polygonal elements.

**THE SURANAL PLATE AS A VALVE.** The modalities of articulation of the suranal plate of *Juliaecarpus* with the posterior part of the thecal frame and with the supracentralia, and the fact that the lateral margins of this plate seem to have been blunt in cross-section, suggest that the suranal plate was probably capable of a certain degree of vertical movement in life, perhaps acting as a flexible lid to seal partially the anal opening and control waste disposal, or as an aid in the regulation of gas exchanges through a pumping action of the gut (Prof. R. L. Parsley, pers. comm.).

That the suranal plate may have played an important role in gas exchange is plausible, considering the fact that the theca of *Juliaecarpus* does not show openings other than the posterior anus. Primitive cornutes display a diverse array of body openings (e.g. sutural pores, cothurnopores, lamellipores, etc.: see Ubaghs, 1968) which are likely to have functioned as respiratory structures (see elaboration of this argument in the chordate interpretation of stylophorans provided by Jefferies, 1986).

Unlike primitive cornutes, ankyroids rarely display thecal openings (apart from the anus). Thus, the evolutionary history of stylophorans may have witnessed a shift in the gas exchange functions from the thecal pores to other parts of the body (e.g. anus, integument, appendage). The perforated stereom of the integuments and, perhaps to a lesser extent, that of the marginalia and of the aulacophore may also have been involved in gas exchange, although this argument is highly speculative.

### The aulacophore as a locomotory device

As stated in the introduction, I regard the aulacophore as the homologue of an echinoderm ambulacrum (Sumrall, 1997). However, I

also believe that most, if not all of the stylophorans used their aulacophores as a locomotory organ.

I agree with Jefferies & Prokop (1972) that the hollow nature and perforated stereom texture of the ossicles, paired plates and styloid in such stylophorans as *Reticulocarpus* may have represented further adaptations for reducing body weight. However, as already explained above, I question the validity of their arguments concerning the occurrence of a short aulacophore. As discussed in the anatomical description, none of the observed specimens of *Juliaecarpus* shows the inside of the styloid and of the ossicular spikes. Therefore, their hollow nature, although plausible, cannot be corroborated by direct observations. In addition, their stereom texture is less porous than that of *Reticulocarpus*.

I concur with Jefferies & Prokop (1972), Jefferies (1975, 1981, 1984, 1986), Jefferies *et al.*, 1987, Woods & Jefferies (1992) and Cripps & Daley (1994) that several morphological features of the stylophorans indicate that they may have moved in the direction of the appendage (i.e. anteriorly according to the anatomical orientation adopted in the present work). As pointed out by Cripps & Daley (1994), the articulated appendage may also have had an anchoring function. As in the case of *Reticulocarpus* and *Prokopicystis* (and most other cornute stylophorans), the distal part of the aulacophore of *Juliaecarpus* must have behaved as a rigid, rod-like structure in life, as suggested by the presence of flat interossicular articular surfaces.

The aulacophore of *Juliaecarpus* could probably move horizontally and vertically thanks to the high degree of flexibility of its proximal region. As in other stylophorans, the bulk of the musculature was probably concentrated in the lumen of the articulated rings of the proximal part of the aulacophore, which probably represented the main motor during locomotion (Jefferies & Prokop, 1972; Jefferies, 1984, 1986; Jefferies *et al.*, 1987; Woods & Jefferies, 1992).

Contrary to Jefferies & Prokop (1972) and Jefferies (1986), however, I consider vertical thrusts of the styloid and ossicular spikes within the sediment to have been poorly effective for movement (as indicated by the fact that the spikes are mostly flattened laterally and show a slightly pronounced keel posteriorly), but highly effective to cut a way open through the mud. Lateral movements of the partially buried intermediate and distal parts of the aulacophore, on the other hand, may have resulted in a more effective lateral pushing action against the substrate. This is because during the lateral thrusts, the entire lateral surfaces of the styloid and ossicular processes were in contact with the mud. The power strokes were made more effective by the rigid articulations between adjacent ossicles and between the most proximal ossicle and the styloid. This functional interpretation is applied also to *Reticulocarpus*.

To sum up, left and right lateral thrusts can be visualised as power strokes exerting an alternating clockwise and anticlockwise 'rowing' action, whereas return strokes consisted mainly of vertical, upward and downward movements enabling the animal to free its aulacophore from mud and to lower it down within sediment. Ruta & Bartels (1998) have recently suggested that a similar alternating series of vertical thrusts (presumably not actively involved in locomotion) and lateral thrusts (exerting a dragging action) occurred in the locomotory cycle of the anomalocystitid mitrate *Rhenocystis latipedunculata* Dehm, 1932 from the Lower Devonian of Germany.

I hypothesize that, at the beginning of each lateral push within the sediment, the theca of *Juliaecarpus* rotated slightly in a direction opposite to that of the thrust and slightly forward (anatomically anterior). As explained below, this yawing component of the movement was probably reduced by the elongation of the theca and by the fact that its centre of mass was likely to be close to the thecal

aulacophore insertion. The position of the theca was perhaps readjusted at the beginning of the successive power stroke, when the 'rowing' action of the aulacophore exerted a lateral thrust in the opposite direction with respect to that of the preceding power stroke.

It is possible that the comparatively more elongate theca of *Juliaecarpus* and its higher degree of bilateral symmetry with respect to *Reticulocarpus* prevented excessive yaw while the animal pulled itself along on the surface of the sea floor (for a comparison with the functional adaptations in mitrates see the comprehensive discussion of the biomechanics of these animals in Jefferies, 1984). That yaw was reduced during locomotion is also suggested by the fact that the centre of mass of the theca of *Juliaecarpus* probably lay somewhere at the level of its anterior half, where the thecal frame reaches its maximum height and width and where the marginalia are comparatively thicker than in more posterior parts of the theca. This region, being close to the theca/aulacophore insertion, was perhaps less likely to swing laterally about a hypothetical vertical axis passing through the anterior thecal excavation.

Rolling and pitching components of the movement were presumably greatly reduced or even absent. This is mainly due to the fact that if, as I believe, locomotion was achieved essentially through lateral thrusting actions of the intermediate and distal parts of the aulacophore (*contra* Jefferies & Prokop, 1972 and Jefferies, 1986 but in partial agreement with the conclusions presented by Jefferies *et al.*, 1987, Daley, 1992 and Woods & Jefferies, 1992), then no vertical components of the reaction forces of the sediment to the movements of the aulacophore could be transmitted to the theca.

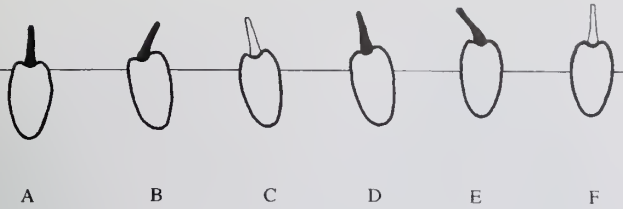
It is possible that such vertical components were slightly more effective when the aulacophore was lowered down within the mud or extracted from it. However, in the downward thrust, the pointed processes of the styloid and ossicles presumably penetrated through the superficial layers of mud with minimum effort. Furthermore, the aulacophore moved essentially through the uppermost layers of the sediment in the upward thrust, where cohesion forces acting between particles of mud were strongly reduced by the high water content.

Thus, friction was negligible during the vertical movements of the aulacophore, because of the slashing action of the spikes and because of the relatively high fluidity of the sediment. The reaction forces to the vertical thrusts exerted by the latter, therefore, were presumably weak. In addition, the flat ventral side of the theca and the occurrence of lateral flanges in *Juliaecarpus* probably prevented or greatly reduced the tilting of the theca (see also above), thus reducing the risk of it sinking into the substrate (for analogous adaptations in other cornutes see Jefferies & Prokop, 1972, Jefferies *et al.*, 1987, Daley, 1992, Woods & Jefferies, 1992 and Cripps & Daley, 1994).

In conditions of maximum ventral flexion of the proximal part of the aulacophore, the spike-like processes pointed backward, or backward and slightly downward. Thus, *Juliaecarpus* may have anchored itself more firmly, for the whole appendage was inserted within relatively dense layers of sediment well below the level of the sea bottom. Such a posture may have been effective in a regime of occasional and particularly strong water currents. Friedrich (1993) proposed a similar anchoring function for the appendage of cinctan echinoderms.

In conclusion, the locomotory cycle of *Juliaecarpus* can be visualized as a series of clockwise and anti-clockwise lateral thrusts of the stiff, intermediate and distal parts of the aulacophore within mud, alternating with vertical movements in the water column, perhaps a few microns off the surface of the sea-floor (Fig. 8). A wide variety of movements could be performed through combination of horizontal and vertical flexions of the tetramerous rings. A clockwise lateral thrust was probably followed by an upward lift of the appendage (which was thus released from the mud), by its partial rotation in an





**Fig. 8** *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Reconstruction of a hypothetical locomotory cycle. The horizontal black line is an imaginary reference direction. **A**, locomotion begins: the aulacophore is lowered down within mud and represented by a blackened rod. **B**, first power stroke: the aulacophore is pushed rightward against mud while the theca yaws slightly anti-clockwise and moves forward while pivoting on its left antero-lateral angle. **C**, first return stroke: the aulacophore (represented by a white rod) is freed from mud and rotated leftward. **D**, the aulacophore is lowered down within mud. **E**, second power stroke: the aulacophore is pushed leftward against mud while the theca yaws slightly clockwise and moves forward while pivoting on its right antero-lateral angle. **F**, second return stroke: the aulacophore is freed from mud and rotated rightward.

anti-clockwise direction (perhaps bringing the aulacophore parallel to the oro-anal axis), by a downward thrust within the sediment (facilitated by the shape of the styloid and ossicles), and finally by a lateral pushing action within the mud in an anti-clockwise direction. During alternating clockwise and anti-clockwise lateral thrusts, the theca of *Juliaecarpus* probably yawed very slightly about a vertical axis passing through or close to the theca/aulacophore insertion, so that its antero-lateral angles moved slightly anterior.

However, yawing, rolling and pitching components of the movements were perhaps negligible, so that the theca was relatively stable during locomotion. The lateral flanges of *Juliaecarpus* may have partially prevented sliding of the theca in a posterior direction, although their poor development in comparison with those of *Reticulocarpos* indicates that they were probably scarcely effective as friction-generating devices.

I point out that, as in previous reconstructions of the locomotory cycle of stylophorans (see especially Jefferies, 1984 and Woods & Jefferies, 1992), no accurate estimate of the speed and of the distance covered by the animal at the end of each power stroke can be provided. Therefore, the position occupied by *Juliaecarpus* at the end of a cycle is only speculative.

Based on the relative proportions of the theca and of the preserved part of the aulacophore I conclude that, as in the case of other cornutes (and perhaps of all stylophorans), locomotion in *Juliaecarpus* was probably not very advantageous from an energy point of view, although it may have allowed the animal to explore adjacent, food-rich patches of the sea-floor (see the next section) and to have changed its position with respect to the water currents. In summary, the life-style of *Juliaecarpus* was perhaps that of a relatively sedentary, suspension and/or detritus feeding, bottom dwelling organism (see also Parsley, 1988, 1991, 1994, 1997, 1998).

### The aulacophore as a feeding organ

With regards to the feeding function of the aulacophore, I accept Parsley's (1988, 1991) view that this structure was probably oriented upstream in the main direction of the water current when the animal fed. *Juliaecarpus* may have exploited food sources in the proximity of its body by moving the rigid, distal part of the appendage laterally, a few microns off the substrate.

With its aulacophore held straight in the water current, *Juliaecarpus* perhaps fed by allowing food particles to enter through the slit-like spaces present between adjacent pairs of distal aulacophore plates. Mitrates, on the other hand, seem to have been able to exploit food particles in suspension more actively than cornutes.

The aulacophore of mitrates (including its distal part) was characterized by a higher flexibility than that of cornutes. According to Parsley (1988, 1991; but see comments in Kolata *et al.*, 1991 and Ruta, 1998, in press), mitrates could arch the distal aulacophore so as to increase the spaces between consecutive segments (the paired cover plates of their distal aulacophores were apparently fused along their medial margins, thus strengthening the whole appendage and making it more effective as a locomotory organ when it pushed against mud).

As explained in the anatomical section, whether the cover plates of the distal aulacophore of *Juliaecarpus* could open in life (as in the case of the cornute genus *Phyllocystis* Thoral, 1935 and few other stylophorans) is difficult to ascertain (Ubaghs, 1968, 1969, 1981; Jefferies, 1968, 1986). It is also proposed that the stirring action exerted by the styloid and ossicular spikes may have brought particulate food in suspension.

The recurved styloid and ossicular spikes of *Juliaecarpus* probably enhanced the gripping action of the aulacophore by pointing in the direction opposite to that of the water current flow (i.e. the spikes would point in a downstream direction) when the animal fed by holding its appendage in the currents.

Waste disposal was perhaps facilitated by slight vertical movements of the suranal plate (see above) and by the fact that, given the position of the animal in the water currents, its faeces were dragged away from the body at the rear end of the theca.

## COMPARISONS

### Similarities and differences in the thecal plating and aulacophore

In this section, *Juliaecarpus* is compared in detail with a number of other ankyroid stylophorans. Such comparisons do not aim to identify shared derived features, although they provide a taxonomic framework for a revised phylogeny of these organisms. As specified in the introduction, a formal numerical character analysis of the stylophorans is not presented in this work.

Among the cornute-like stylophorans placed by Parsley (1997, 1998) in his order Ankyroida, the genera *Reticulocarpos*, *Beryllia* and *Domfrontia* are discussed at length here, for they show closer resemblance to *Juliaecarpus* than other ankyroids do. I also briefly compare *Juliaecarpus* with *Nanocarpus*, which represents a generalized ankyroid with several skeletal features foreshadowing the morphological condition found in later, presumably more derived stylophorans.

*Juliaecarpus* is similar to *Reticulocarpos hanusi* from the Llanvirn of Bohemia (Fig. 9) in the general aspect and proportions of the theca, in the shape and relative lengths of the marginalia and in the morphology of the styloid and ossicles. However, external anatomical differences between these two taxa are numerous and can be summarized as follows:

1. The thecal outline of *Juliaecarpus* is more bilaterally symmetrical than that of *Reticulocarpos*. Corresponding pairs of marginalia, especially the more posterior ones, are almost equal in shape and length and the oro-anal axis is almost aligned with the longitudinal axis of the aulacophore. In addition, the lateral thecal margins

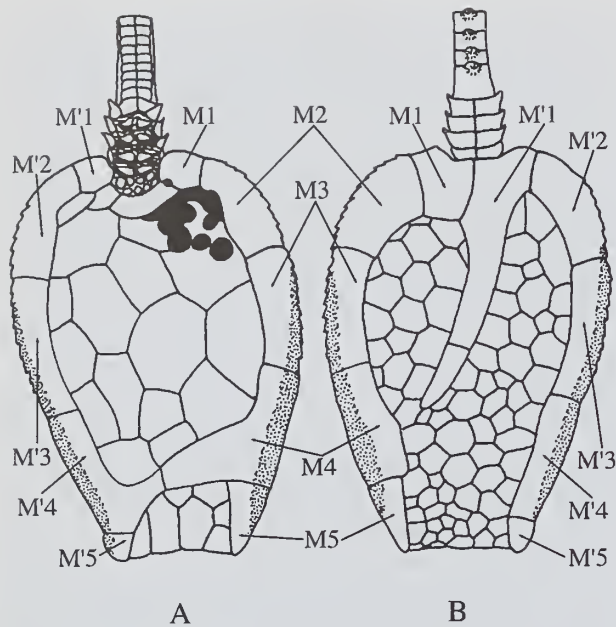


Fig. 9 *Reticulocarpus hanusi* Jefferies & Prokop. Middle Ordovician, Llanvirn, Sárka Formation, Czech Republic. Schematic reconstruction of external aspect. A, dorsal view. B, ventral view (redrawn and modified after Jefferies & Prokop, 1972 and Cripps & Daley, 1994).

of *Juliaecarpus* show their maximum degree of curvature at the level of plates  $M'_2$  and  $M_2$ , whereas in *Reticulocarpus*, such margins are more strongly convex at the level of  $M_3$  and  $M'_3$ , on the right side of the theca, and of  $M'_2$  and  $M'_3$ , on its left side. In addition, the dorso-lateral projections of the marginalia of *Juliaecarpus* are slightly to much wider than their ventral projections, whereas in *Reticulocarpus*, the difference in width between the two kinds of projections is much smaller.

2. Unlike *Reticulocarpus*, *Juliaecarpus* possesses a large suranal plate. This plate is probably not unique to *Juliaecarpus*, as I shall explain below, because an enlarged plate occupying the posterior part of the dorsal integument seems to have been present also in *Beryllia* and *Domfrontia* (see discussion of these genera below).
3. In *Juliaecarpus*, plates  $M'_4$  and  $M_4$  do not send medial projections forming a dorsal bar as in *Reticulocarpus*. In the stylophoran phylogeny presented by Parsley (1997, 1998), the presence of a dorsal bar characterizes a clade uniting *Reticulocarpus*, *Prokopocystis* and *Hanusia*, contrary to the hypotheses of relationships presented by Cripps (1991) and Cripps & Daley (1994) (but see also Daley, 1992).
4. Plates  $M'_2$  and  $M_2$  of *Juliaecarpus* are less strongly convex laterally than their namesakes in *Reticulocarpus* and their dorso-lateral projections are slightly wider than those of more posterior marginalia. The dorso-lateral projections of  $M'_2$  and  $M_2$  contribute only in part to the antero-lateral angles of the theca, whereas in some other ankyroids (but not in *Reticulocarpus*), these marginalia send more strongly developed medial branches forming most of the antero-lateral angles of the theca.
5. The length of the posterior process of  $M'_1$  in *Juliaecarpus* is almost twice the length of the posterior zygial plate; such a process is also slightly wider than the ventral projections of the marginalia throughout its length and its posterior end lies slightly

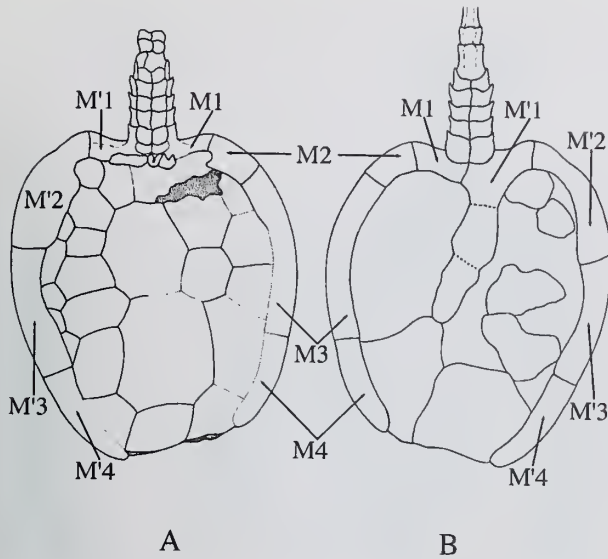
posterior to the suture between  $M_3$  and  $M_4$  and slightly anterior to that between  $M'_3$  and  $M'_4$ . In *Reticulocarpus*, on the other hand, the  $M'_1$  process is comparatively shorter and stouter than that of *Juliaecarpus* and its posterior half is less wide than the ventral projections of the marginalia; furthermore, its posterior end lies anterior to both the  $M_3/M_4$  and the  $M'_3/M'_4$  sutures. In addition, the posterior zygial plate of *Reticulocarpus* probably did not contact the thecal frame (see discussion below).

6. The lateral margins of  $M_2$  and  $M'_2$  in *Juliaecarpus* carry shallow denticulations, as opposed to the pronounced, saw-like serrations present along the lateral margins of  $M_2$ ,  $M'_2$ ,  $M_3$  and  $M'_3$  in *Reticulocarpus*.
7. Plates  $M'_5$  and  $M_5$  of *Juliaecarpus*, assuming their correct identification, are comparatively much smaller than their namesakes in *Reticulocarpus* and much narrower than more anterior marginalia. In *Reticulocarpus*, these plates also differ in shape and size, whereas in *Juliaecarpus*, they are almost mirror images of each other.
8. In *Juliaecarpus*, the transition from the retiform stereom texture on the median part of the dorso-lateral projections of the marginalia to the striated texture on the peripheral flange is more gradual than in *Reticulocarpus* and no cancellose or irregular stereom is interposed between these two kinds of textures.
9. The peripheral flange of *Juliaecarpus* is less developed than that of *Reticulocarpus* and appears to have possessed comparatively shallower lateral fringes and less irregular trabeculae; in addition, it seems to have been confined mainly to the anterior half of the lateral margins of the thecal frame.
10. Some of the supracentralia of *Juliaecarpus*, especially those on the anterior half of the dorsal integument, approach a bilaterally symmetrical arrangement and it is always possible to distinguish some larger plates in a central position flanked by longitudinal rows of smaller plates comprised between the marginal frame and the oro-anal axis. Conversely, the supracentralia of *Reticulocarpus* are not arranged according to a particular pattern.
11. The spike-like processes on the styloid and ossicles of *Juliaecarpus* are comparatively less high, less recurved and more laterally flattened than those of *Reticulocarpus* and pointed almost exactly downward rather than downward and rearward in life. The stereom texture of the styloid and ossicles is slightly more compact and consists of comparatively smaller perforations in *Juliaecarpus* than in *Reticulocarpus*.

The internal aspect of the theca permits more limited comparisons between *Juliaecarpus* and *Reticulocarpus*. At the level of the zygial bar, the most obvious difference between these two genera is the fact that in *Juliaecarpus*, the ridge on the dorsal surface of the zygial process of  $M'_1$  does not extend as far forward as in *Reticulocarpus*, in which such a ridge reaches the suture between  $M_1$  and  $M'_1$ . The preservation of the internal side of  $M_1$  and  $M'_1$  in *Juliaecarpus* is not as detailed as in *Reticulocarpus*. A comparison between the reconstruction of these plates in *Juliaecarpus* and the reconstruction provided by Jefferies & Prokop (1972) for *Reticulocarpus* highlights major differences in the morphology of this region of the theca in the two ankyroids.

Two other stylophorans, *Beryllia miranda* and *Domfrontia pissotensis*, both from the Llandeilo of France, reveal interesting similarities with *Juliaecarpus*. As in *Juliaecarpus*, some of the supracentralia of both *Beryllia* and *Domfrontia*, especially those aligned along the oro-anal axis, are slightly to much larger than the remaining supracentralia. In the case of *Beryllia*, the supracentralia which occupy the anterior third of the dorsal integument are





**Fig. 10** *Beryllia miranda* Cripps & Daley. Middle Ordovician, Llandeilo, Pissot Formation, France. Schematic reconstruction of external aspect. **A**, dorsal view. **B**, ventral view (redrawn and modified after Cripps & Daley, 1994).

arranged in broadly transverse rows (e.g. Cripps & Daley, 1994: pl. 2, fig. 5).

In the reconstruction of *Beryllia* provided by Cripps & Daley (1994), the thecal frame shows four left and four right marginal plates ( $M'_5$  and  $M_5$  are presumably absent) (Fig. 10). In the same reconstruction, a subpentagonal and an irregularly parallelogram-like plate of subequal size appear along the posterior margin of the dorsal integument and roof over the obliquely oriented anal opening.

However, at least one of the specimens of *Beryllia* figured by Cripps & Daley (1994: pl. 2, fig. 5) shows a transversely expanded, subrectangular supra-central plate between the posterior ends of  $M'_4$  and  $M_4$ . The plate in question carries an irregular fringe along its posterior margin and the average size of its stereom mesh pores is slightly larger than that of other dorsal integument plates. It may be homologous with the suranal plate of *Juliaecarpus* but its outline and relative position with respect to the surrounding plates are poorly defined.

The following skeletal features distinguish *Juliaecarpus* from *Beryllia*:

1. Higher thecal length/width ratio. Based on the measurements provided by Cripps & Daley (1994), *Beryllia* shows a thecal length/width ratio of about 1:2, as opposed to the ratio value of 1:72 reported in *Juliaecarpus*.
2. Smaller length difference between the left and the right lateral thecal margins, accompanied by more bilaterally symmetrical thecal outline and less oblique position of the anal opening. In *Beryllia*, the theca is slightly asymmetrical, due to length difference between the left and the right marginalia. Such difference characterizes all cornute-like ankyroids and indicates that the process of symmetrization of the thecal outline must have preceded the acquisition of paired marginalia of equal (or subequal) shape and size. *Juliaecarpus* exemplifies a stage of this process, in that the presence of an almost bilaterally symmetrical theca is accompanied by almost complete symmetrization of the more posterior pairs of marginalia, whereas the anterior marginalia

(especially  $M'_2$  and  $M_2$ ) are still markedly different (see also comparison with *Nanocarpus* below).

3. Less pronounced convexity of lateral thecal margins (see also point 2 above).
4. Lesser elongation of  $M_3$  with respect to other marginalia (see also point 1 above).
5. Dorso-lateral projections of marginalia wider than their ventral projections (see also point 1 in the comparison with *Reticulocarpus*).
6. Greater difference in shape and size between the ventral projections of  $M_1$  and  $M_2$ . The ventral projections of these marginalia appear to be subequal in *Beryllia*, but markedly different in *Juliaecarpus*.
7. Much smaller difference in length between  $M'_2$  and  $M_2$  (see also point 2 above).
8. Slenderer, straighter and comparatively more elongate zygial process of  $M'_1$  (see also discussion of this structure below).
9. Less clear demarcation between  $M'_1$  and its zygial process. While in *Beryllia* the posterior zygial process of  $M'_1$  widens abruptly in its anterior part to become confluent with this plate, in *Juliaecarpus* the boundary between  $M'_1$  and its process is less clearly evident (see description of the internal surface of this plate above).
10. Adoral plates longer than wide and separated by a leftward concave suture. The occurrence of a median adoral in *Beryllia* is possible, based on the poor material figured by Cripps & Daley (1994). The left and right adoralia of *Beryllia* are wider than long and, in comparison with those of *Juliaecarpus*, they are much smaller than the dorso-lateral projections of  $M'_1$  and  $M_1$ .
11. Apparently larger number of broad, polygonal, more regularly arranged plates on the anterior third of the ventral integument. In *Beryllia*, only a few large polygonal supra-centralia in a subcentral position are visible. These are flanked by irregularly shaped plates, apparently more numerous on the left than on the right. As pointed out in the anatomical description above, the supra-centralia of *Juliaecarpus* form transverse rows of elements arranged in a bilaterally symmetrical (or nearly so) pattern on the anterior half of the dorsal integument (see also point 11 in the comparison with *Reticulocarpus*).
12. Strongly developed, recurved, spike-like styloid and ossicular processes. The styloid and ossicles of *Beryllia* possess low, poorly pronounced keel-shaped longitudinal processes, clearly different from the conical processes of *Juliaecarpus* (see also point 11 in the comparison with *Reticulocarpus*).

The material of *Domfrontia* is less well preserved than that of *Beryllia*, but it does permit limited comparisons with *Juliaecarpus*. As in the case of *Juliaecarpus* and *Beryllia*, it is difficult to ascertain the precise number of lateral marginal plates, due to the poor preservation of the rearmost ends of the thecal frame (Fig. 11).

The inside of what I interpret as a possible suranal plate is partly visible in the holotype of *Domfrontia* (Cripps & Daley, 1994: pl. 1, fig. 5). The right part of such a plate, assuming its correct identification, is hidden by one of the rearmost preserved infracentralia. The visible portion of it shows a more regular outline than the suranal of *Juliaecarpus*, a less extensive posterior fringe attached to an apparently semielliptical posterior margin and an almost straight, thickened anterior margin. However, unlike the suranal of *Juliaecarpus* and, perhaps, *Beryllia*, the like-named plate of *Domfrontia* does not seem to show a remarkably different stereom texture with respect to other integument plates.

The most important morphological differences when *Domfrontia* is compared with *Beryllia* and *Juliaecarpus* are as follows:

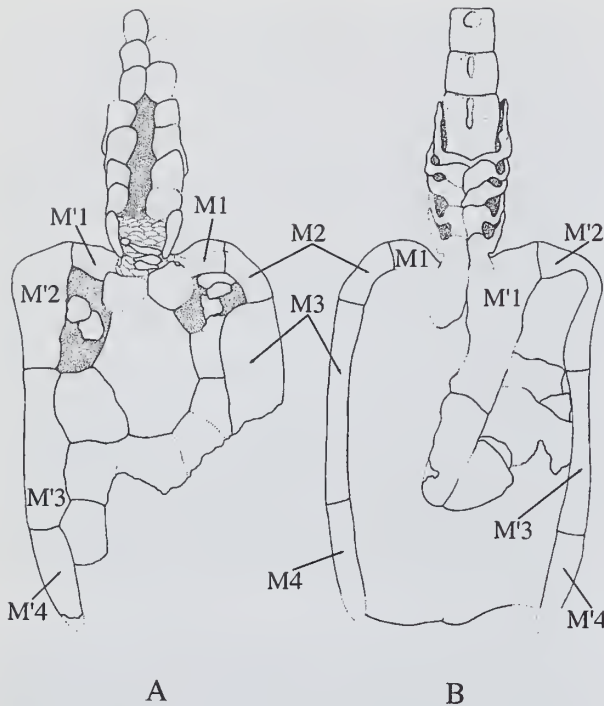


Fig. 11 *Domfrontia pissotensis* Cripps & Daley. Middle Ordovician, Llandeilo, Pissot Formation, France. Schematic reconstruction of external aspect. A, dorsal view. B, ventral view (redrawn and modified after Cripps & Daley, 1994).

1. According to the reconstruction provided by Cripps & Daley (1994), *Domfrontia* possesses almost straight lateral thecal margins. As a result, the anal opening is approximately as wide as the theca. Proportions and relative lengths of the marginalia of *Domfrontia* are similar to those of *Beryllia*, but differ remarkably from those of *Juliaecarpus*. The convexity of the lateral thecal margins of *Juliaecarpus* is somewhat intermediate between that of *Beryllia* and that of *Domfrontia*.
2. The zygial process of  $M'_1$  in *Domfrontia* is comparatively wider and shorter than that of both *Beryllia* and *Juliaecarpus*. Likewise, the preserved part of the posterior zygial plate of *Domfrontia* suggests that this plate is stouter in this ankyroid than in the other two genera.
3. The styloid and ossicles of *Domfrontia* are shaped like bulges with a subelliptical to subcircular outline and carry a poorly defined median longitudinal keel with a semicircular to parabolic profile.
4. The ventral projection of  $M_1$  is expanded posteriorly in *Domfrontia*, but not in *Beryllia* and only to a very limited extent in *Juliaecarpus*.

The number of marginal plates in such genera as *Juliaecarpus*, *Reticulocarpus*, *Beryllia* and *Domfrontia*, as well as their relative position and shape, gives support to Parsley's (1991, 1997, 1998) suggestion that several lineages within the ankyroids underwent reduction in the number of marginalia through decrease in size and subsequent loss of the rearmost plates. A brief comparison with the ankyroid *Nanocarpus dolambii* Ubaghs, 1991, from the lower Ordovician of southern France is interesting in this respect (Fig. 12).

Except for asymmetries in the thecal frame due to the relatively small size of  $M_2$  and elongation of  $M'_3$ , the theca of *Nanocarpus* is

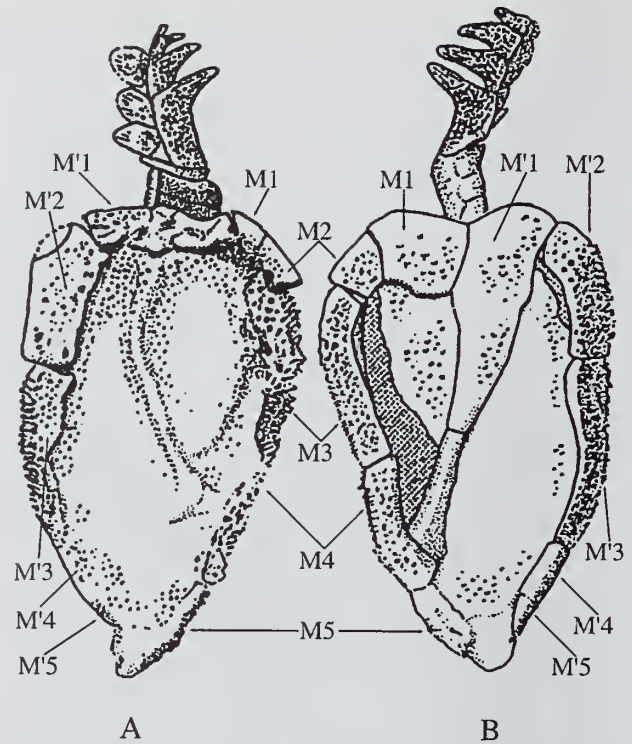


Fig. 12 *Nanocarpus dolambii* Ubaghs. Lower Ordovician, Lower Arenig, Schistes de Saint-Chinian, France. Schematic reconstruction of external aspect. A, dorsal view. B, ventral view (redrawn and modified after Ubaghs, 1991).

similar to that of *Juliaecarpus*. From a purely morphological point of view, *Nanocarpus* can be considered as a fairly generalized cornute-like ankyroid in which the theca retained asymmetries as in more primitive cornutes. In *Nanocarpus*, the rearmost marginalia, especially  $M_5$ , are still relatively large with respect to more anterior marginalia, as opposed to the situation observed in *Reticulocarpus* and *Juliaecarpus*. On the other hand,  $M'_4$  and  $M_4$  are shorter than  $M'_3$  and  $M_3$ , and  $M'_2$  and  $M_2$  differ greatly in size.

An interesting feature observed in some of the specimens of *Nanocarpus* figured by Ubaghs (1991) is the presence of a posterior plate visible between  $M'_5$  and  $M_5$ . Although poorly preserved, this element seems to be homologous with the suranal plate of *Juliaecarpus*. However, it is difficult to say whether it was flexibly articulated with the rest of the thecal frame in life.

It is possible to hypothesize that, in the evolutionary history of the ankyroid stylophorans, thecal asymmetries were drastically reduced through the loss of the posterior marginalia, subsequent elongation of the marginalia occupying an intermediate position along the lateral margins of the thecal frame and, finally, acquisition of a more bilaterally symmetrical outline. A suranal plate, as explained below, may have been acquired in a number of ankyroids through enlargement and rearward displacement of a posterior supracentral plate which became flexibly articulated both with the dorsal integument and with the medial margins of the dorso-lateral projections of the most posterior marginalia.

As far as the ventral surface of the theca is concerned, the posterior zygial plate and posterior zygial process of *Nanocarpus* are similar in shape and general proportions to those of *Juliaecarpus*, except that in *Nanocarpus*, the posterior zygial process of  $M'_1$  is slightly curved



and decreases rapidly in width distally and the posterior end of the posterior zygial plate is comparatively wider than in *Juliaecarpus*.

### Suranal plate and stylophoran orientation

The occurrence of a well developed suranal plate in *Juliaecarpus* and, perhaps, also in *Beryllia* and *Domfrontia* (see discussion above) requires further comments on the orientation of cornutes (including cornute-like ankyroids) with respect to mitrates. Workers supporting the chordate interpretation of stylophorans (synthesis in Jefferies, 1986) homologize the plano-concave surface of the mitrate theca with the dorsal side of the cornute theca. Given this orientation, it may be argued that the suranal plate is homologous with the subanal plate observed in such early mitrates as *Chinianocarpus thoralis* Ubahgs, 1961, *Peltocystis cornuta* Thoral, 1935 and, perhaps, *Vizcainocarpus dentiger* Ruta, 1997 (see also Ubahgs, 1968, 1969). In these mitrates, the subanal plate occupies the posterior part of the plano-concave surface of the theca and floors the anal opening. As in the case of the suranal plate, there are indications that, at least in *Chinianocarpus* and *Peltocystis*, the subanal plate was flexibly articulated with the theca (Ubahgs, 1969).

In their discussion of the phylogenetic position of *Reticulocarpus* and the origin of mitrates, Jefferies & Prokop (1972) proposed that one of the supracentralia lying close to the mouth opening in derived, mitrate-like cornutes increased in size and gave rise to either the large subanal of such primitive mitrates as *Chinianocarpus* and *Peltocystis* (and, perhaps, *Vizcainocarpus*) or the rearmost element of the plano-concave surface of other mitrates (e.g. mitrocystitids and anomalocystitids; see also Ruta 1998, in press).

However, as already explained in the introduction, the bulk of anatomical evidence (arguments in Ubahgs, 1981, Kolata *et al.*, 1991, Parsley, 1991, 1997, Sumrall, 1997 and Lefebvre *et al.*, 1998), based mainly on a comparison between the aulacophore, adoral plates, apophyses and zygial/septum complex of cornutes and the like-named structures of mitrates, strongly supports the convex-side-up orientation of the mitrates as well as the homology between the convex surface of their thecae and the dorsal side of the cornute thecae.

Therefore, I regard the suranal plate of *Juliaecarpus* as a modified posterior dorsal integument plate, not homologous with the subanal plate of certain primitive mitrates. The suranal plate was perhaps not unique to *Juliaecarpus*. I tentatively suggest that its occurrence may represent a shared derived feature of a group of ankyroids including *Juliaecarpus*, *Beryllia* and *Domfrontia*. From the morphological comparisons outlined above, it is clear that these taxa show certain skeletal features in common. Enlargement of supracentralia on the posterior part of the dorsal integument (forming or not an almost regular spatial arrangement) and reduction or loss of the most posterior pair of marginalia are other possible shared characters of this group. A close relationship of these ankyroids with the clade (*Hanusia* + (*Reticulocarpus* + *Prokopocystis*)) (all these genera share a dorsal bar; see Parsley, 1997, 1998) is possible, considering the overall similar proportions and morphological characters of the theca and aulacophore in *Juliaecarpus* and *Reticulocarpus*.

However, I point out that, according to Parsley's (1997, 1998) phylogenetic analysis, *Beryllia* is the sister taxon to a clade comprising *Chinianocarpus* and the peltocystids (including *Peltocystis* as the most basal representative of this group of mitrates; see also Jefferies, 1973, 1986 and Jefferies & Lewis, 1978). In addition, Parsley (1997, 1998) did not include in his analysis *Domfrontia*, ranked among the poorly known or incomplete taxa. Clearly, the mixture of primitive and derived features found in *Juliaecarpus* requires a substantial reassessment of the polarity of a number of characters.

### Morphological variation in the zygial bar

Among the ankyroid stylophorans, the genera *Beryllia*, *Domfrontia*, *Prokopocystis* and *Reticulocarpus* differ from other representatives of this group in the morphology of their zygial bar. The unusual configuration of this structure in the above-mentioned taxa deserves further considerations.

*Reticulocarpus*, *Prokopocystis* and *Domfrontia* were reconstructed as having an incomplete zygial bar (Jefferies & Prokop, 1972; Cripps, 1989a; Cripps & Daley, 1994). In particular, *Reticulocarpus* seems to have had a small somatic plate (posterior zygial plate) attached to the posterior zygial process of  $M'_1$ . In Cripps' (1989a) reconstruction of *Prokopocystis*, only the posterior zygial process of  $M'_1$  seems to have been present and no trace of a posterior plate attached to it has been recorded. In their reinterpretation of *Domfrontia*, Cripps & Daley (1994) reconstructed the zygial bar of this stylophoran as being similar to that of *Reticulocarpus*.

However, with the possible exception of *Reticulocarpus*, the incompleteness of the zygial bar in *Domfrontia* and *Prokopocystis* is based on the interpretation of very poor material. None of the figured specimens of these two ankyroid genera clearly shows the boundaries of the posterior zygial plate. In a note published a few years before the formal description of *Reticulocarpus* by Jefferies & Prokop (1972) (Jefferies, pers. comm.), Ubahgs (1969) clearly stated that the zygial bar in two of the specimens of *Reticulocarpus* examined by him was apparently incomplete.

It is difficult to ascertain whether the incompleteness (if any) of the zygial bar is evidence of its progressive reduction and final disappearance in derived cornutes and, therefore, of the fact that the zygial/septum complex is not homologous in all stylophorans.

The peculiar zygial bar of *Beryllia* as reconstructed by Cripps & Daley (1994) suggests that this structure had a separate somatic plate in contact with a posterior right infracentral element, and that its anterior two-thirds comprised, in turn, a posterior plate and a short, stout process of  $M'_1$ . Cripps & Daley (1994: 108) state that the strut of *Beryllia* is '... most clearly visible on NHM E63499a', but the figured specimen in question does not provide unequivocal evidence of a tripartite zygial bar. I re-examined the specimen in question and the remaining material of *Beryllia* in the collections of the London Natural History Museum. The specimens were cast using black-stained latex.

My own observations do not match Cripps & Daley's (1994). In particular, the zygial bar in NHM E63499 is too poorly preserved for its boundaries and general shape to be reconstructed. In particular, I could find no evidence of tripartition and no clear delimitation of the posterior zygial plate from the thecal frame. The impression left by the zygial bar on the dorsal integument of another specimen (NHM E63496b; Cripps & Daley, 1994: pl. 2, fig. 5) suggests that, in fact, the zygial bar of *Beryllia* had a slender shape and a sinuous course and that its rearmost end lay closer to the posterior right part of the thecal frame than in the reconstruction provided by Cripps & Daley (1994). In these respects, the bar is similar to that of such ankyroids as *Amygdalotheca griffiei* Ubahgs, 1969 from the lower Ordovician of southern France.

That the zygial bar of *Beryllia* may have consisted of a posterior process of  $M'_1$  and of a posterior zygial plate is plausible, although not certain. However, I favour the latter interpretation, based in particular on the visible course of the bar in specimen NHM E63496b.

In summary, the specialized features of the zygial bar reported in several ankyroid species ought to be confirmed by discovery of better preserved material. *Juliaecarpus* shows the primitive condition for the ankyroids in possessing a posterior somatic plate articulated with the inner margins of the thecal frame. If my conclu-

sions are correct, the character distribution in above-mentioned ankyroids will have to be reconsidered, especially when the origin of mitrates from their cornute ancestors is taken into account.

## CONCLUSIONS

Together with *Beryllia*, *Domfrontia* and *Reticulocarpos*, the new stylophoran *Juliaecarpus milnerorum* gen. et sp. nov. from the late Ashgill (late Rawtheyan) Upper Ktaoua Formation of Morocco ranks among the most bilaterally symmetrical stylophoran echinoderms. Following recent phylogenetic work by Parsley (1997, 1998), *Juliaecarpus* is an ankyroid, that is, a stylophoran with a separate zygial plate not belonging to the thecal frame and with well-developed, spike-shaped styloid and ossicular processes.

The most outstanding skeletal feature of *Juliaecarpus* is the presence of a large suranal plate flexibly articulated with the rear-most part of the thecal frame and dorsal integument. Such a plate may have enabled *Juliaecarpus* to regulate the pumping action of the gut by acting as a vertically movable, lid-like structure and to control waste disposal. A suranal plate was probably present also in the ankyroid genera *Beryllia* and *Domfrontia*, as suggested by the occurrence of a large, apparently continuous dorsal area revealing stereom structure at the posterior end of the theca.

A comparison with several ankyroids strengthens the view that, during the evolutionary history of the stylophorans, asymmetries in the thecal outline and in the marginalia, inherited from primitive (and often boot-shape) cornutes, became progressively less accentuated and were eventually lost in many forms (Ubaghs, 1968; Jefferies, 1986; Cripps, 1989b; Parsley, 1991, 1994, 1997, 1998; Ruta, 1998, in press). The acquisition of a progressively more bilaterally symmetrical thecal outline presumably preceded a complete symmetrization of the paired marginalia. Several stages of this process are exemplified by a number of cornute-like ankyroids. For instance, *Juliaecarpus* displays a high degree of bilateral symmetry in the theca, but asymmetries can still be observed at the level of some of the marginalia, especially  $M_1$ ,  $M'_1$ ,  $M_2$  and  $M'_2$ .

Acquisition of bilateral symmetry probably occurred several times independently in the stylophorans, as recent phylogenetic analyses and re-assessment of stylophoran thecal plate homologies suggest (Parsley, 1997, 1998; Lefebvre *et al.*, 1998; Dr B. Lefebvre, pers. comm.; Ms M. Martí-Mus, pers. comm.).

As in the case of *Reticulocarpos*, *Juliaecarpus* was probably capable of resting on the surface of the muddy sea-floor aided in this by the weight-bearing capacity of the sediment (Jefferies & Prokop, 1972). Nearly bilaterally symmetrical shape, small size, flat ventral surface of the theca, peripheral flange (albeit reduced in size in comparison with that of *Reticulocarpos*) and highly perforated skeletal plates all seem to account for this life-style.

Movement perhaps involved a downward thrusting and a lateral pushing action of the aulacophore within the sediment followed by an upward return stroke enabling the animal to free its aulacophore from the mud. Alternating clockwise and anti-clockwise lateral thrusts represented the active component of the locomotory cycle, whereas upward and downward movements, as well as lateral movement in the water column just above the sea-floor, allowed *Juliaecarpus* to readjust the position of its aulacophore between two successive power strokes. Several skeletal features of the theca and aulacophore suggest that yawing, rolling and pitching components of the movement were absent or much reduced.

Stability in the water currents was probably achieved through a combination of factors: 1) suction forces acting along the flat ventral

side of the theca; 2) reduction of water turbulence due to the low, gently convex lateral profile of the theca and possible production of eddies immediately above the theca/aulacophore junction, both effects resulting in water pressure increase (Bernoulli effect); 3) anchoring function of the recurved styloid and ossicular spikes, perhaps enhanced by the ability of the animal to bend the proximal part of its aulacophore ventralward and rearward to a considerable degree.

*Juliaecarpus* probably fed by holding its aulacophore upstream in the water current (see also Parsley, 1988, 1991). Food particles were brought in suspension by the stirring action of the aulacophore and forced to pass through the narrow spaces between adjacent pairs of cover plates.

*Juliaecarpus* adds to the taxonomic similarities between middle to late Ordovician faunas from Morocco and coeval faunas from several European regions. It also adds to the diversity of early cornute-like ankyroids, combines features of several previously described taxa and prompts a reassessment of the polarity of many characters within the stylophoran echinoderms. It is hoped that a revised character analysis of the whole group can yield information on the phylogenetic significance of this ankyroid.

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## REFERENCES

- Beisswenger, M. 1994. A calcichordate interpretation of the new mitrate *Eumitrocystella savilli* from the Ordovician of Morocco. *Paläontologische Zeitschrift*, Stuttgart, **68**: 443–462.
- Caster K. E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpid Echinodermata. *Bulletin of American Paleontology*, Ithaca, **34**: 1–47.
- Chauvel, J. 1971. Les Echinodermes Carpoïdes du Paléozoïque inférieur marocain. *Notes du Service Géologique de Maroc*, Rabat, **31**: 49–60.
- 1981. Etude critique de quelques échinodermes stylophores du Massif Armoricain. *Bulletin de la Société Géologique et Minéralogique de Bretagne*, Rennes, **13**: 67–101.
- 1986. *Milonicystis kerformei* n. gen. n. sp. Un nouvel échinoderme homalozoaire de l'Ordovicien armoricain. *Hercynica*, Rennes, **2**: 79–81.
- & Nion, J. 1977. Échinodermes (Homalozoa: Cornuta et Mitrata) nouveaux pour l'Ordovicien du Massif Armoricain et conséquences paléogéographiques. *Geobios*, Villeurbanne, **10**: 35–49.
- Craske, A. J. & Jefferies, R. P. S. 1989. A new mitrate from the upper Ordovician of Norway, and a new approach to subdividing a plesion. *Palaeontology*, London, **32**: 69–99.
- Cripps, A. P. 1989a. A new stem-group chordate from the Llandeilo of Czechoslovakia and the cornute-mitrate transition. *Zoological Journal of the Linnean Society*, London, **96**: 49–85.
- 1989b. A new genus of stem chordate (Cornuta) from the Lower and Middle Ordovician of Czechoslovakia and the origin of bilateral symmetry in the chordates. *Geobios*, Villeurbanne, **22**: 215–245.
- 1990. A new stem craniate from the Ordovician of Morocco and the search for the sister-group of the craniata. *Zoological Journal of the Linnean Society*, London, **100**: 27–71.
- 1991. A cladistic analysis of the cornutes (stem-chordates). *Zoological Journal of the Linnean Society*, London, **102**: 333–366.



- & Daley, P. E. J. 1994. Two cornutes from the Middle Ordovician (Llandilo) of Normandy, France, and a reinterpretation of *Milonicystis kerfernei*. *Palaeontographica*, Stuttgart, **232**: 99–132.
- Daley, P. E. J. 1992. Two new cornutes from the Lower Ordovician of Shropshire and Southern France. *Palaeontology*, London, **35**: 127–148.
- 1996. The first solute which is attached as an adult: a Mid-Cambrian fossil from Utah with echinoderm and chordate affinities. *Zoological Journal of the Linnean Society*, London, **117**: 405–440.
- Dehm, R. 1932. Cystoiden aus dem rheinischen Unterdevons. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie. Beil.-Bd., Abteilung A*, Stuttgart, **69**: 63–93.
- Destombes, J., Holland, C. H. & Willefert, S. 1985. Lower Palaeozoic rocks of Morocco. In: Holland, C. H. (ed.), *Lower Palaeozoic of north-western and west central Africa*: 91–336. John Wiley & Sons, London.
- & Willefert, S. 1988. The Ordovician-Silurian boundary in Morocco. In: Cocks, L. R. M. & Rickards, R. B. (eds), *A Global Analysis of the Ordovician-Silurian Boundary*: 165–170. *Bulletin of the British Museum (Natural History)*, London, *Geology Series*, **43**: 5–394.
- Donovan, S. K. in press. Echinoderms and calcichordates. In: Savazzi, E. (ed.), *Functional morphology of the invertebrate skeleton*. John Wiley & Sons, Chichester.
- Fleming, J. 1828. *A History of British Animals, exhibiting the descriptive Characters and systematical Arrangement of the Genera and Species of Quadrupeds, Birds, Reptiles, Fishes, Mollusca, and Radiata of the United Kingdom*. Bell & Bradfutes, Edinburgh, pp 565.
- Friedrich, W.-P. 1993. Systematik und Funktionsmorphologie mittelkambrischer Cincta (Carpoidea, Echinodermata). *Beringeria*, Würzburg, **7**: 3–190.
- Gee, H. E. 1996. *Before the backbone. Views on the origin of the vertebrates*. Chapman & Hall, London, pp 346.
- Gill, E. D. & Caster, K. E. 1960. Carpodid echinoderms from the Silurian and Devonian of Australia. *Bulletins of American Paleontology*, Ithaca, **41**: 5–71.
- Gislén, T. 1930. Affinities between the Echinodermata, Enteropneusta and Chordonia. *Zoologiska Bidrag*, Stockholm, **12**: 199–304.
- Havlíček, V. 1990. Mediterranean and Malvinokaffric Provinces: new data on the Upper Ordovician and Lower Silurian brachiopods. *Casopis pro Mineralogii a Geologii*, Prague, **35**: 1–13.
- Hicks, H. 1872. On some undescribed fossils from the Menevian Group. *Quarterly Journal of the Geological Society of London*, London, **28**: 173–185.
- Jaekel, O. 1901. Über Carpoideen, eine neue Klasse von Pelmatozoen. *Zeitschrift der Deutschen Geologischen Gesellschaft*, Berlin, **52**: 661–677.
- 1918. Phylogenie und System der Pelmatozoen. *Paläontologische Zeitschrift*, Stuttgart, **3**: 1–128.
- Jefferies, R. P. S. 1968. The Subphylum Calcichordata (Jefferies 1967), primitive fossil chordates with echinoderm affinities. *Bulletin of the British Museum (Natural History)*, London, *Geology Series*, **16**: 243–339.
- 1969. *Ceratocystis perneri* Jaekel—a Middle Cambrian chordate with echinoderm affinities. *Palaeontology*, London, **12**: 494–535.
- 1973. The Ordovician fossil *Lagynocystis pyramidalis* (Barrande) and the ancestry of amphioxus. *Philosophical Transactions of the Royal Society of London, Series B*, London, **265**: 409–469.
- 1975. Fossil evidence concerning the origin of the chordates. *Symposium of the Zoological Society of London*, London, **36**: 253–318.
- 1981. In defence of the calcichordates. *Zoological Journal of the Linnean Society*, London, **73**: 351–396.
- 1984. Locomotion, shape, ornament and external ontogeny in some mitrate calcichordates. *Journal of Vertebrate Paleontology*, Norman, **4**: 292–319.
- 1986. *The ancestry of the vertebrates*. British Museum (Natural History), London, and Cambridge University Press, Cambridge, pp 376.
- 1997. A defence of the calcichordates. *Lethaia*, Oslo, **30**: 1–10.
- & Lewis, D. N. 1978. The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. *Philosophical Transactions of the Royal Society of London, Series B*, London, **282**: 205–323.
- , Lewis, M. & Donovan, S. K. 1987. *Protocystites menevensis* – a stem-group chordate (Cornuta) from the Middle Cambrian of South Wales. *Palaeontology*, London, **30**: 429–484.
- & Prokop, R. J. 1972. A new calcichordate from the Ordovician of Bohemia and its anatomy, adaptations and relationships. *Biological Journal of the Linnean Society*, London, **4**: 69–115.
- Kolata, D. R., Frest, T. J. & Maples, R. H. 1991. The youngest carpodid: occurrence, affinities and life mode of a Pennsylvanian (Morrowan) mitrate from Oklahoma. *Journal of Paleontology*, Lawrence, **65**: 844–855.
- & Jollie, M. 1982. Anomalocystiid mitrates (Stylophora, Echinodermata) from the Champlainian (Middle Ordovician) Guttenberg Formation of the Upper Mississippi Valley Region. *Journal of Paleontology*, Lawrence, **56**: 531–565.
- Lefebvre, B., Racheboeuf, P. & David, B. 1998. Homologies in stylophoran echinoderms. In: Mooi, R. & Telford, M. (eds), *Echinoderms: San Francisco*: 103–109. Balkema, Rotterdam.
- Parsley, R. L. 1988. Feeding and respiratory strategies in Stylophora. In: Paul, C. R. C. & Smith, A. B. (eds), *Echinoderm phylogeny and evolutionary biology*. 347–361. Clarendon Press, Oxford.
- 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). *Bulletins of American Paleontology*, Ithaca, **100**: 5–57.
- 1994. Mitrocystitid functional morphology, evolution and their relationships with other primitive echinoderm classes. In: David, B., Guille, A., Féral, J.-P. & Roux, M. (eds), *Echinoderms through time*: 167–172. Balkema, Rotterdam.
- 1997. The echinoderm classes Stylophora and Homoiostelea: non Calcichordata. In: Waters, J. A. & Maples, C. G. (eds), *Geobiology of echinoderms. Paleontological Society Papers 3*: 225–248. The Paleontological Society, Pittsburgh.
- 1998. Taxonomic revision of the Stylophora. In: Mooi, R. & Telford, M. (eds), *Echinoderms: San Francisco*: 111–117. Balkema, Rotterdam.
- Peterson, K. J. 1995. A phylogenetic test of the calcichordate scenario. *Lethaia*, Oslo, **28**: 25–38.
- Philip, G. M. 1979. Carpodids – echinoderms or chordates? *Biological Reviews*, Cambridge, **54**: 439–471.
- Ruta, M. 1997. A new mitrate from the lower Ordovician of southern France. *Palaeontology*, London, **40**: 363–383.
- 1998. Interrelationships of the anomalocystitid mitrates. *Ph.D. dissertation*, University of London, 336 pp.
- in press. A cladistic analysis of the anomalocystitid mitrates. *Zoological Journal of the Linnean Society*, London.
- & Bartels, C. 1998. A redescription of the anomalocystitid mitrate *Rhenocystis latipedunculata* from the Lower Devonian of Germany. *Palaeontology*, London, **41**: 771–806.
- Smith, A. B. 1980. Stereom microstructure of the echinoid test. *Special Papers in Paleontology*, London, **25**: 1–81.
- Sumrall, C. D. 1997. The role of fossils in the phylogenetic reconstruction of Echinodermata. In: Waters, J. A. & Maples, C. G. (eds), *Geobiology of echinoderms. Paleontological Society Papers 3*: 267–288. The Paleontological Society, Pittsburgh.
- , Sprinkle, J. & Guensburg, T. E. 1997. Systematics and paleoecology of late Cambrian echinoderms from the western United States. *Journal of Paleontology*, Lawrence, **71**: 1091–1109.
- Swofford, D. L. 1993. *PAUP. Phylogenetic Analysis Using Parsimony. Version 3.1.1*. Illinois Natural History Survey, Champaign, pp 257.
- Thoral, M. 1935. *Contribution à l'étude paléontologique de l'Ordovicien inférieur de la Montagne Noire*. Imprimerie de la Charité, Montpellier, pp 363.
- Ubachs, G. 1961. Un échinoderme nouveau de la classe des Carpoïdes dans l'Ordovicien inférieur du département de l'Herault (France). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **253**: 2565–2567.
- 1963. *Cothurnocystis* Bather, *Phyllocystis* Thoral and an undetermined member of the order Soluta (Echinodermata, Carpoidea) in the uppermost Cambrian of Nevada. *Journal of Paleontology*, Lawrence, **37**: 1133–1142.
- 1967. Le genre *Ceratocystis* Jaekel (Echinodermata, Stylophora). *Paleontological Contributions of the University of Kansas*, Lawrence, **22**: 1–16.
- 1968. Stylophora. In: Moore R. C. (ed.), *Treatise on invertebrate paleontology. Part 5. Echinodermata I* (2): 496–565. Geological Society of America, Boulder and University of Kansas Press, Lawrence.
- 1969. *Les échinodermes carpoïdes de l'Ordovicien inférieur de la Montagne Noire (France)*. *Cahiers de Paléontologie*. Éditions du Centre National de la Recherche Scientifique, Paris, pp 112.
- 1981. Reflexions sur la nature et la fonction de l'appendice articulé des carpoïdes Stylophora (Echinodermata). *Annales de Paléontologie, Invertébrés*, Paris, **67**: 33–48.
- 1987. Échinodermes nouveaux du Cambrien moyen de la Montagne Noire (France). *Annales de Paléontologie, Invertébrés*, Paris, **73**: 1–27.
- 1991. Deux Stylophora (Homalozoa Echinodermata) nouveaux pour l'Ordovicien inférieur de la Montagne Noire (France Méridionale). *Paläontologische Zeitschrift*, Stuttgart, **65**: 157–171.
- 1994. Échinodermes nouveaux (Stylophora, Eocrinoida) de l'Ordovicien inférieur de la Montagne Noire (France). *Annales de Paléontologie, Invertébrés*, Paris, **80**: 107–141.
- Woods, I. S. & Jefferies, R. P. S. 1992. A new stem-group chordate from the Lower Ordovician of South Wales, and the problem of locomotion in boot-shaped cornutes. *Palaeontology*, London, **35**: 1–25.